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Late Quaternary Vegetation History of Northern North America Based on Pollen, Macrofossil, and Faunal Remains

Histoire de la végétation de la fin du Quaternaire de la partie nord de l'Amérique du Nord basée sur les pollens, les macrofossiles et les restes d'animaux

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Résumé de l'article

Les cartes des biomes établies entre le dernier maximum glaciaire et les temps modernes sont présentées. La répartition des biomes en 18 ka BP était probablement en équilibre avec le climat comme les distributions modernes, mais les biomes durant la déglaciation étaient probablement en déséquilibre. La configuration de la calotte glaciaire exerçait un fort contrôle sur le climat jusque vers 7 ka BP. Les tendances climatiques régionales peuvent être estimées à partir des changements observés dans la répartition des biomes, mais en période de déséquilibre leur distribution sous-représente le réchauffement estival. À cause du refroidissement estival de 2 à 4 °C durant l'Holocène, depuis les derniers 3 à 5 ka, la distribution des biomes au cours de l'Holocène moyen et inférieur et la composition des espèces sont similaires aux déplacements de l'équilibre futur lié au réchauffement, du moins pour les régions qui sont déglacées depuis longtemps. Les taux de migration des biomes anciens furent de l'ordre de 100 à 200 m par année. Si ces taux se maintiennent dans le futur, les biomes pourraient se déplacer de 10 à 20 km dans la plupart des régions au cours du prochain siècle. L'obstacle majeur à l'utilisation des conditions qui prévalent durant l'Holocène, pour l'estimation des conditions futures, est que les étés chauds sont accompagnés d'hivers froids tandis que les futurs étés chauds seront accompagnés d'hivers chauds.

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LATE QUATERNARY VEGETATION HISTORY OF NORTHERN NORTH AMERICA BASED ON POLLEN, MACROFOSSIL, AND FAUNAL REMAINS*

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ABSTRACT Biome maps spanning the interval from the last glacial maximum to modern times are presented. The biome distributions at 18 ka BP were probably as nearly in equilibrium with climate as are the modern distributions, but deglacial biomes were probably in disequilibrium. Ice sheet configuration was a strong control of climate until 7 ka BP. Regional climate trends can be inferred from changing biome distributions, but during periods of disequilibrium, biome distributions under-represent summer warming. Because of summer cooling by 2-4 °C during the Holocene, largely in the last 3-5 ka, middle and certain early Holocene biome distributions and species compositions are reasonable analogues of future equilibrium displacements due to equivalent warming, at least in areas that were long-since deglaciated. Past biome migration rates in response to rapid regional warming during deglaciation were mainly in the range of 100-200 m per year. If these rates pertain in the future, biomes may shift 10-20 km in most regions over the next century. A major impediment to using former Holocene conditions as a guide to future conditions is that warmer Holocene summers were accompanied by colder winters, whereas warmer future summers will be accompanied by warmer winters.

RÉSUMÉ *Histoire de la végétation de la fin du Quaternaire de la partie nord de l'Amérique du Nord basée sur les pollens, les macrofossiles et les restes d'animaux.* Les cartes des biomes établies entre le dernier maximum glaciaire et les temps modernes sont présentées. La répartition des biomes en 18 ka BP était probablement en équilibre avec le climat comme les distributions modernes, mais les biomes durant la déglaciation étaient probablement en déséquilibre. La configuration de la calotte glaciaire exerçait un fort contrôle sur le climat jusque vers 7 ka BP. Les tendances climatiques régionales peuvent être estimées à partir des changements observés dans la répartition des biomes, mais en période de déséquilibre leur distribution sous-représente le réchauffement estival. À cause du refroidissement estival de 2 à 4 °C durant l'Holocène, depuis les derniers 3 à 5 ka, la distribution des biomes au cours de l'Holocène moyen et inférieur et la composition des espèces sont similaires aux déplacements de l'équilibre futur lié au réchauffement, du moins pour les régions qui sont déglacées depuis longtemps. Les taux de migration des biomes anciens furent de l'ordre de 100 à 200 m par année. Si ces taux se maintiennent dans le futur, les biomes pourraient se déplacer de 10 à 20 km dans la plupart des régions au cours du prochain siècle. L'obstacle majeur à l'utilisation des conditions qui prévalent durant l'Holocène, pour l'estimation des conditions futures, est que les étés chauds sont accompagnés d'hivers froids tandis que les futurs étés chauds seront accompagnés d'hivers chauds.

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INTRODUCTION

In considering the distribution of vegetation during the Late Wisconsin maximum, not only beyond the Laurentide Ice Sheet but in the Cordilleran region as well, we must stress at the outset that paleoecology, whether of plants or of animals, is more complex and its data more obscure than the glacial geology we have been describing. We are dealing here with ecosystems, natural dynamic systems that consist of the entire biotic community and its environment (Flint, 1971: p. 500).

Reconstructions of former vegetation and associated terrestrial mammal communities of Late Quaternary time have been the focus of much research effort in North America (Wright, 1983; Ritchie, 1984, 1987a; Bryant and Holloway, 1985; Graham *et al.*, 1987; COHMAP members, 1988; Huntley and Webb, 1988; FAUNMAP, 1994; Williams *et al.*, 2004; Strong and Hills, 2005). Early attempts date from the dawn of Quaternary pollen stratigraphy (Sears, 1935; Deevey, 1949; references in Ogden, 1965), which predated the advent of radiocarbon dating, and hence of secure chronologies. For lack of firm chronology and other methodological reasons, these pre-radiocarbon studies are now of historical interest only. Still, it is a mark of progress to note that as late as 1955, it was possible to seriously consider that the vegetation south of the ice sheets at the last glacial maximum was little different from present vegetation except very close to the ice margin (Braun, 1955), and that even by 1971 only the vaguest description of vegetation south of the ice sheet could be offered (Flint, 1971: p. 510). Ignoring terrestrial mammals for the moment and considering only paleovegetation studies, the currently available set of data for northern North America and adjacent regions was beginning to be constructed during the 1960s (105 publications). The pace of work increased during the 1970s (174 publications), peaked during the 1980s (316 publications), and declined somewhat in the 1990s (275 publications). The prominent producers of primary data are listed in the Acknowledgements below. During the entire period, research objectives appear to have shifted from addressing more geological questions (broad environmental sequences and the history of climate change) to more ecological questions (individual species histories and forest dynamics).

The most recent attempts at paleogeographic synthesis have tended to focus on the last glacial maximum (Jackson *et al.*, 2000) – a time when orbital conditions were similar to present, but boundary conditions such as ice extent and atmospheric CO_2 content were greatly different – and on 6000 years ago (Vance in Gajewski *et al.*, 2000) – a time when boundary conditions were essentially the same as today (except that CO_2 was at pre-industrial levels), but when summer radiation receipt in high latitudes was substantially greater than today while winter radiation was proportionately lower. The purpose or relevance of recent work is commonly expressed in terms of the need to have empirical reconstructions to compare against computer model simulations of biomes and climates, because these models are one basis for forecasting future biome displacements due to global warming. However, there is also intrinsic value in understanding environmental history: for example, in providing historical background for understanding modern genetic diversity within plant and animal species, in assessing theories about the great mammalian extinctions that resulted in the loss of 70% of North American large mammal species about 10 000 radiocarbon years ago (10 ka BP), in seeking correlates with major events in human (archaeological) history, and as probable examples of the environmental impacts of former climate changes. The increased pace of publication of new information about the Late Quaternary history of northern North America, both geological and biological, has motivated the Geological Survey of Canada to use a geographical information systems (GIS) approach to paleogeographic reconstruction in the hope of facilitating frequent amendments.

This study presents a sequence of maps illustrating the reestablishment of the continental vegetation cover after the last glacial maximum, which occurred about 18 ka BP (21 400 calendar years ago; all ages below are in radiocarbon years except where rates of change are discussed and calendar ages are then used; see Stuiver *et al.* (1998) for conversions). It also examines biome migration rates and compares the most thermophilous biome positions and compositions with those of the warmest parts of the Sangamonian Interglaciation, when temperatures considerably exceed those of the postglacial thermal maximum. The maps extend south to 39 °N latitude, the southernmost extent of the last continental ice sheet. They extend west to northeastern Siberia, which at the last glacial maximum was contiguous with unglaciated Alaska and Yukon Territory, the area known collectively as Beringia, and east to Iceland. Maps are shown for 18 ka BP, for 14 ka BP, and for each 1000-year time step thereafter. The deglaciation sequence – that is, the abiotic paleogeography of ice, sea, and lake cover – are taken from Dyke *et al.* (2002; also in Dyke, 2004), who present maps using a 500-year time step. These maps and the supporting chronological data, along with the vegetation maps contained herein, can also be viewed on the Quaternary Paleoenvironments web site of the Geological Survey of Canada (http://ess.nrcan.gc.ca/2002_2006/rcvcc/j27/1_1_e.php).

The present vegetation cover can be mapped at a variety of levels of detail ranging from hectare-scale "stands" (*e.g.,* a jackpine stand) to regional assemblages and to provincial-scale biomes. Biomes are distinctive plant and animal communities that are named for their dominant plant types (*e.g.,* boreal forest, grassland). Most paleovegetation maps use biome-level units, although assemblage-level mapping is possible where sites are dense. Because biomes are not spatially homogeneous formations, the number of biomes recognized in any mapping exercise will vary according to the amount of data available, the resolution of the data source, and the scale and purpose of mapping. Biome compositions are known to have changed through time, as discussed below.

The distribution of biomes is controlled by climate. Given sufficient moisture, plant distributions are mainly dictated by temperature, most significantly by factors such as the length of the growing season, mean temperature of the warmest month, and secondarily by minimum winter temperatures. Thus, the northern limit of woody shrubs – willow, heather, blueberry, arctic avens – within the High Arctic herb tundra coincides with a July mean temperature of 3 °C (Edlund and Alt, 1989); the northern limit of shrub tundra in Canada – the limit of dwarf birch and alder – coincides with a July mean

temperature of 7.5 °C; latitudinal treeline – the boundary between forest tundra and shrub tundra – coincides with a July mean temperature of 10 °C, which in turn is fixed by the mean summer position of the Arctic Front (Bryson, 1966); the boundary between boreal forest and forest tundra coincides with the 13 °C July isotherm (Edlund, 1986); and the southern boundary of the boreal forest, which approximates the mean winter position of the Arctic Front, roughly follows the 17.5 °C July isotherm (Hare and Thomas, 1974). In the east, this boundary may be more effectively prescribed by the -40 °C minimum winter isotherm, because this threshold evidently determines the northern limit of temperate deciduous trees (Arris and Eagleson, 1989). Shoots are killed by intracellular freezing below that temperature in these trees, but not in boreal species. Where the climate is warm enough to support trees but where moisture is insufficient, grassland and steppe biomes are arranged along a gradient of decreasing moisture and increasing temperature. These biomes occur where the total annual precipitation is <0.5 m and where moisture balance is negative. The boundary between the boreal forest and the aspen parkland on the Canadian Prairies, for example, coincides closely with the zero contour of P-PET (precipitation minus potential evapotranspiration), whereas the boundary between the aspen parkland and the grassland coincides with the -15 cm contour (Hogg, 1994).

Therefore, the former distribution of biomes might be used to infer past climates. However, during times of climate change, biome limits may not have been in equilibrium with the transient climate. Although plant mortality may quickly follow a deleterious climate change at the limit of the geographical range of a species, rates of plant migration and die-off are limited by physiographic and edaphic (soil) barriers and by biological processes of seed dispersal, seedling establishment, seedling destruction, and survival of plants through vegetative reproduction. Thus, numerical biome models that assume instantaneous plant migration in response to future climate change predict greatly different biomes than do those that do not, particularly with respect to treeline movements (Lenihan and Neilson, 1995; Solomon and Kirilenko, 1997). Similarly, numerical reconstructions of past climates from pollen data assume that former plant species distributions, not just biome boundaries, were in equilibrium with former climates. Multi-proxy data are increasing revealing that plant colonization may have lagged climate warming by millennia and that maximum summer temperatures did not necessarily coincide with the most thermophilous vegetation development. For example, Miller *et al.* (2005) showed that lacustrine productivity and summer temperature peaked long before the most diverse and apparently most thermophilous plant cover was established on eastern Baffin Island. This is not to say that individual plants do not respond quickly, even seasonally, to climate, but rather that the equilibrium response of plant assemblages may be delayed by centuries to millennia (Williams *et al.*, 2002, Shuman *et al.*, 2004). It follows, therefore, that while climate trends may be inferred from former changes of vegetation cover, a proper assessment of the sensitivity of vegetation to climate change requires an independent reconstruction of climate history. In Canada, such reconstructions are emerging mainly from the study of fossil chironomids, the remains of species of non-biting midges (flies), which are aeroplankton that are abundantly preserved in lake sediments and whose aquatic larvae require certain water temperatures for survival (Walker and Pellatt, 2003). Available reconstructions are cited below where appropriate.

Former vegetation cover is here classified into 15 biomes. These will be generally familiar to most North American readers and are defined, as used here, in Table I.

DATA SOURCES AND METHOD

The biome reconstructions are based on radiocarbon-dated paleontological records of three kinds: (1) pollen stratigraphic sequences (1385 sites); (2) plant macrofossils (892 sites); and (3) terrestrial mammal macrofossils (4262 dates <25 ka [tabulated]; 4050 dates <18.5 ka [mapped]). Each data set comprises independent spreadsheets that are interactive with the online GIS-based versions of the paleobiome maps. That is, querying of a site symbol will open the relevant portion of a database. The spatial density of sites is the best measure of the confidence that one might place in a biome interpretation, followed by the internal consistency of the site classifications within a biome (a site classification may differ from the biome interpretation). In places, additional sites will undoubtedly lead to amended interpretations. Additional sites in the modern forest tundra, shrub tundra, and southern herb tundra of central and eastern Canada are those most needed from a biome mapping perspective, along with additional sites dating to 14 ka BP and older.

The online pollen database lists the site name, publication source (author, date), and geographic co-ordinates for each site (only key and representative works are cited below). For each millennial time slice, the following three columns of information are given: Description, Biome, and Association. The entries under “Description” attempt to capture faithfully the published interpretations of the pollen assemblages; *e.g.,* “Alder-birch shrub tundra (*Alnus-Betula*-Ericaceae zone)” and “White pine forest with spruce, fir, birch, elm, ash, and cedar.” These descriptions were analysed in a separate spreadsheet by sorting, synonymising (*e.g., Picea* zone = spruce zone) and generalizing (*e.g.,* White pine forest with spruce, fir, birch, elm, ash, cedar = Mixed Forest) in order to reduce the more than 1500 unique descriptions to the 15 biomes listed in Table I. Only the Biome column is used here for mapping. However, plant assemblages (*e.g.,* White Pine-Spruce-Fir-Birch-Elm-Ash-Cedar, in the mixed forest example just cited) are listed in the database where possible in order to retain more fully the interpretations of the original analysts and to aid in more detailed future mapping. Hence, the database captures most of what is available in the regional palynological literature, which deals mainly with qualitative interpretation. No attempt is made here to treat the vast numerical data sets (pollen counts) such as are available in the North American Pollen Database and are the subject of analyses by others (Williams *et al.*, 2004).

Pollen stratigraphies are subject to a number of chronological uncertainties. Despite increasing use of more precise dating methods (accelerator mass spectrometric dating of small plant macrofossils from lake sediment), most interpretations

TABLE I

Biomes used in the paleovegetation maps

Biome	Characteristics
Herb tundra	A treeless area lacking shrubs other than small, prostrate willows and dominated by bare ground and herbs, typically sedge, grass, and sage with a variety of forbs; includes fellfield.
Shrub tundra	A treeless area with a nearly continuous cover of sedge, grass, sage, and forbs along with prostrate and semi-erect willows as well as one or more additional shrubs, chiefly dwarf birch, alder, and juniper, in increasing order of required warmth.
Alpine tundra	Similar to herb or shrub tundra but occurring at high elevations.
Forest tundra	A zone transitional between shrub tundra and boreal forest. That is, a continuous ground cover of herb and shrub vegetation with open stands of erect trees, typically spruce, larch, and (or) poplar (birch in Iceland).
Boreal forest	Nearly continuous cover of trees dominated by northern conifers (mainly spruce, jackpine, larch, and fir) and northern hardwoods (mainly birch, aspen, poplar), broken by wetlands.
Boreal parkland	Open stands of boreal forest trees growing in ground covers dominated by herb and (or) lichen. Includes the modern aspen parkland at the southern fringe of the western boreal forest in the Prairie Provinces and the lichen woodland (open spruce forest) of the eastern boreal forest, which grades to forest tundra.
Subalpine forest	The conifer-dominated forest in mountainous terrain of the Cordillera. Dominated by subalpine fir, Engelmann spruce, mountain hemlock, lodgepole pine, and whitebark pine in northern ranges; limber pine, bristlecone pine, and juniper farther south.
Conifer forest	A cover of conifer trees different in composition from modern boreal, subalpine, or interior forests. Typically dominated by lodgepole pine in areas of modern subalpine and interior forests.
Interior forest	The conifer-dominated forest of the relatively dry interior of the Cordilleran region, which occurs south of the western boreal forest and experiences cold winters; typically dominated by Douglas fir, lodgepole pine, whitebark pine and Ponderosa pine, with western hemlock, Engelmann spruce, Sitka spruce, and cedar.
Coast forest	The conifer-dominated forest of the wet coastal ranges and lowlands of the Pacific coast, which experience mild winters; typically dominated by western hemlock, western red cedar, and Sitka spruce with Douglas fir, alder, grand fir, and silver fir.
Mixed forest	Conifer-hardwood assemblages mainly occupying the transition zone between the boreal forest and the deciduous forest of eastern North America. Dominated by boreal elements (conifers and northern hardwoods [birch, beech, elm]) on the north and temperate elements on the south. Includes a diverse mosaic of associations dominated by white pine, hemlock, white cedar, maple, yellow birch, oak, etc.
Deciduous forest	The broad-leaf, temperate, deciduous forest of eastern North America; typically dominated by oak with beech, birch, maple, basswood, hickory, chestnut, ironwood, hemlock and white pine.
Savannah	A zone transitional between grassland and deciduous forest, with oak typically dominating the trees.
Grassland	Treeless or nearly treeless vegetation dominated by grass, sage, or chenopods, grading to steppe with decreasing moisture; includes long- and short-grass prairie.
Steppe	Treeless or nearly treeless semi-desert vegetation of western North America dominated by sagebrush, chenopods, shadscale, and grass, with occasional lodgepole pine, Ponderosa pine, and juniper.

rely on dating of the bulk organic content of lake sediments. In calcareous terrains especially, but also in non-calcareous terrains where organic sedimentation rates were low, bulk sediment dates commonly are too old (Dyke, 2004). Where analysts have subjectively adjusted their pollen zone ages for perceived dating errors, these adjusted dates are used here. However, some of the age assignments are probably in need of further adjustment. In viewing the paleobiome maps, the obvious suspects, some of which are discussed below, are those sites that place warmth-demanding assemblages farther north than do other sites in the same region at a particular time. In some of these cases, the site interpretations conflict with the biome interpretation. Furthermore, age resolution is uneven from study to study, generally being higher in more recent work. In earlier work, the ages of pollen zone boundaries were typically estimated to the nearest millennium, which indicates a perceived uncertainty of about 500 years. In more recent work, the uncertainty is closer to centennial. Where a pollen zone boundary coincides with a mapped time slice, the older pollen zone is used for mapping, because this partly compensates for the tendency of the sediment to date too early.

The online plant macrofossil database lists similar information regarding sites, literature sources, and co-ordinates, followed by entries that give dated taxa, radiocarbon ages, and laboratory codes as “Observations”, with a biome interpretation in the adjacent column. These are directly dated macrofossils and there is commonly only one or a few per site. The more continuous macrofossil data that are available from some lake sediment cores that were analysed for pollen are not included here, because interpretations of these data were incorporated in interpretations of the pollen stratigraphy. Far-travelled materials, such as driftwood recovered from raised beaches in the Arctic, are excluded, because they do not represent the biomes at the collection sites. Because the map

series has a 1000-year time step, all dated fossils that are within 500 years of the times portrayed are plotted on the maps. This wide binning of data leads to an occasional site that plots incongruously within the ice-covered area. Other sites that plot within the ice area are those here judged to have erroneous radiocarbon ages. Plant macrofossils are generally less informative than pollen data for present mapping purposes, because most occurrences indicate only the presence of a single taxon. Thus only biome-level inferences are usually possible. Nevertheless, plant macrofossils are commonly identified to species level, whereas pollen is typically identified only to genus or higher levels. Therefore, plant macrofossils provide welcome supporting evidence particularly at times and places with little or no pollen data. Furthermore, in certain contexts, such as in the fossil packrat (*Neotoma* spp.) middens in the arid American Southwest, plant macrofossil assemblages are thought to represent rather fully the local vegetation and to allow reconstructions that are not possible with pollen data alone (Betancourt *et al.*, 1990).

The fossil mammal database provides a listing of radiocarbon dates, laboratory codes, co-ordinates, literature sources, material and taxon dated, associated taxa, and biome interpretations. As with plant macrofossils, each map displays sites with dates that fall within 500 years of the time slice. Terrestrial mammal fossils allow only biome-level inferences in most instances. These inferences are based on the modern habitat preferences of extant taxa (Banfield, 1977) and on habitats inferred from dietary habits (*e.g.,* grazers, browsers, carnivores) for extinct taxa (Harington, 2003). Like plant macrofossils, the mammal fossils help fill in the maps in the absence of pollen data. In addition, particularly in eastern Beringia and on the Great Plains, the full-glacial to late-glacial mammal fossils provide a view of the regional plant communities that is altogether richer than that indicated solely by the few available pollen records (compare Guthrie, 1985 with Ritchie, 1984).

RESULTS

The biomes familiar to North Americans have existed in nearly modern geographical configurations for only the last 5000-6000 years. Even during that time span, biome boundaries have shifted slightly and their species compositions have changed in response to general late Holocene cooling, particularly during the last 3000 years. For example, boreal elements such as spruce have shown an increase throughout much of the mixed forest biome. Although our present biome-level mapping is too coarse grained and taxonomically too imprecise to recognize association-level changes, we summarize key assemblage changes and distributions below.

Due to the paucity of fossil sites, we assume that the distributions of biomes in North America during the last interglacial period (130 000 to 115 000 years ago) were broadly similar to those of the present day (see discussion below for differences). As the continental ice sheets grew and partially waned at decamillennial intervals during the last glaciation (*ca.* 115 000 to 20 000 years ago), these biomes were necessarily displaced equatorward and changed in species composition. With the possible exception of an extinct species of spruce (*Picea critchfieldii*; Jackson *et al.*, 2000), which appears to have been confined to areas south of 39 °N at the last glacial maximum, all plant taxa herein are those found in modern biomes as far as taxonomic resolution can determine. The extreme displacement of biomes during the Late Pleistocene presumably is that shown on the 18 and 14 ka BP maps. The Laurentide Ice Sheet margin was at or approaching its southernmost limit in most places by about 23 ka BP (Dyke *et al.*, 2002). Therefore, the biome distribution at 18 ka BP was probably as well adjusted to its contemporaneous climate as the modern distribution is to modern climate. After 14 ka, the pace of atmospheric warming and deglaciation quickened. It is less safe to assume that biome distributions were in equilibrium with climate from that time until about 6 ka BP. What follows is a brief sketch of the major changes in biome distributions and their plant and faunal compositions from the last glacial maximum to the present day, followed by a comparison of Holocene and Sangamonian conditions.

GLACIAL MAXIMUM

The climate of the last glacial maximum has been elucidated by general circulation model experiments (COHMAP Members, 1988; Bartlein *et al.*, 1998), which have largely confirmed earlier geological interpretations (Barry, 1983). Over North America, the atmospheric circulation was dominated by a large anticyclone above the continental ice sheet, thus generating easterly winds along the southern margin from the Atlantic to the Pacific. This anticyclonic flow split the jet stream in winter, one branch crossing Beringia and the northern flank of the ice sheet, the other crossing the continent from southern California to the southeastern ice sheet margin. Mid-latitude storms today track along the jet stream, which separates polar from warmer air masses, and, presumably, that was the case in the past. The anticyclone shrank in radius as the ice sheet retreated and probably dissipated with the deglaciation of Hudson Bay about 7.6 ka BP. The western part of the continent was deglaciated earlier than the east. Hence, the western landfall of the jet stream moved northward to its present position in the Alaska Panhandle (southeastern Alaska) relatively early, by 10-11 ka BP. We shall see that this change of atmospheric circulation from 18 ka BP to about 7 ka BP can explain much of the sequence of biome changes from the last glacial maximum to the middle Holocene.

18 ka BP

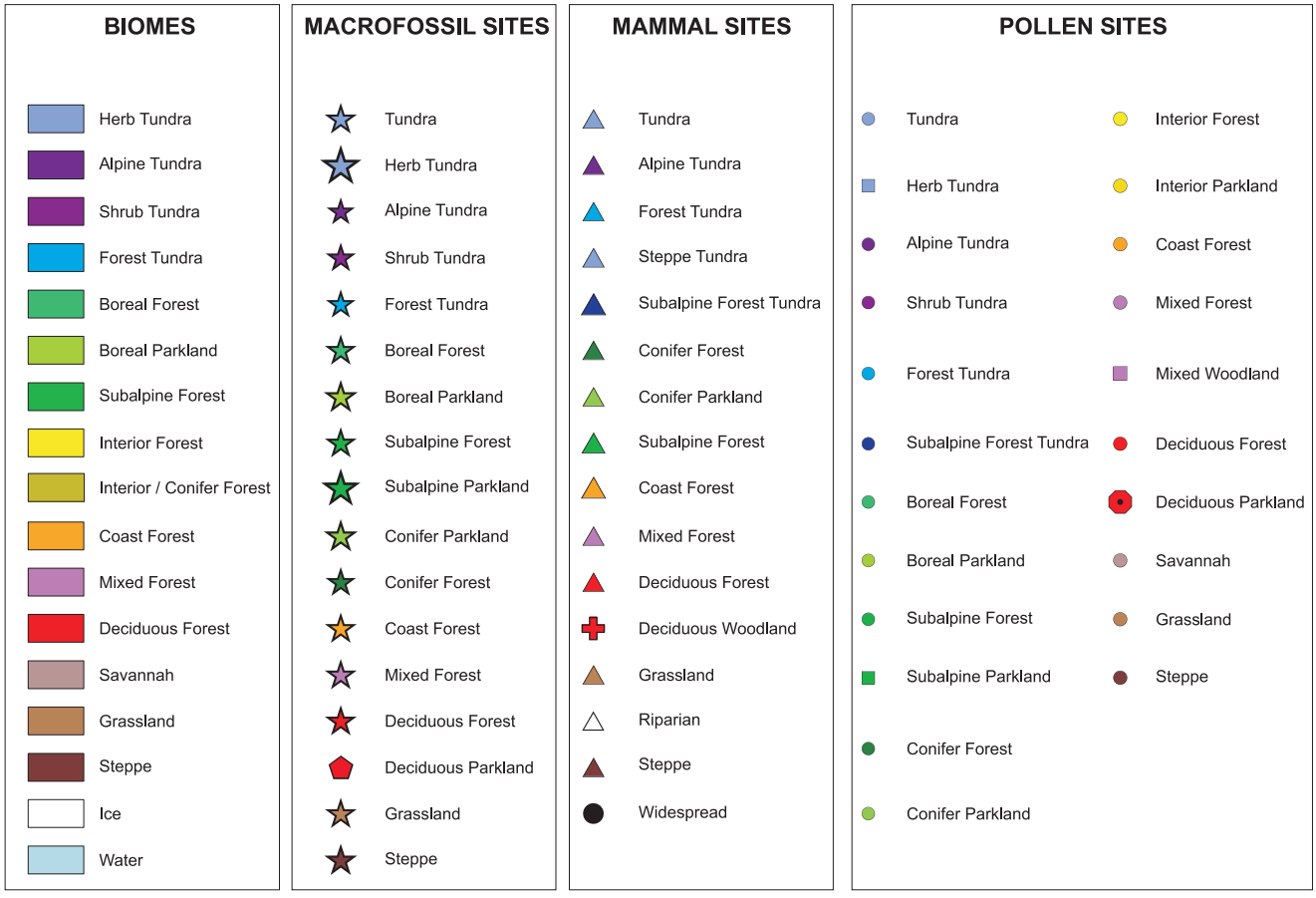
The species that comprise the modern forest and grassland biomes of North America necessarily survived the last glaciation south of the ice sheets. However, the paleontological record of the details of species distribution remains sparse, because of the paucity of sites with appropriate depositional records that extend into this time interval. It is generally conceded that boreal forest species – such as black and white spruce (*Picea mariana* and *P. glauca*), jackpine (*Pinus banksiana*), balsam fir (*Abies balsamea*), larch (*Larix laricina*), balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*) – and mixed forest species – such as eastern white pine (*Pinus strobus*), eastern hemlock (*Tsuga*

canadensis), eastern white cedar (*Thuja occidentalis*), the maples (*Acer* spp.), ashes (*Fraxinus* spp.), oaks (*Quercus* spp.), yellow birch (*Betula alleghaniensis*), ironwood (*Ostrya virginiana*), beech (*Fagus grandifolia*), basswood (*Tilia americana*), and the elms (*Ulmus* spp.) – were displaced to the American South and Southeast (Delcourt and Delcourt, 1981); that coast forest species – such as Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) – were displaced to the coastal ranges of California and Oregon (Hebda and Whitlock, 1997); and that montane-subalpine species – such as subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta*), and mountain hemlock (*Tsuga mertensiana*) – were displaced southward in the Cordillera. There has been more debate about the nature of the vegetation cover on the southern Great Plains during the last glacial maximum, but most current interpretations favour a cover dominated by grassland taxa rather than trees (Holliday, 1987).

At 18 ka BP (Fig. 1), herb tundra with willow (*Salix reticulata*) survived in front of advancing glaciers on the Queen Charlotte Islands of British Columbia (Warner *et al.*, 1982; Blaise *et al.*, 1990), including perhaps areas now below sea level. It has been proposed on DNA evidence that grizzly bears (*Ursus arctos*) survived the last glaciation in this region, including the adjacent archipelago in Alaska, where they are now more genetically allied with the polar bear (*Ursus maritimus*) than are the brown bears of the mainland (Heaton *et al.*, 1996). However no full-glacial fossils of this, or other, terrestrial mammal species have yet been recovered there.

The ice sheet in southwestern British Columbia at 18 ka BP was advancing across lowland terrain that supported a forest of fir and spruce (Clague *et al.*, 1980; Hicock and Lian, 1995). Occurrences of Townsend's vole (*Microtus townsendii*) dated to 18.01 ka BP on southwestern Vancouver Island are in agreement with this interpretation, because this animal occurs today only below alpine treeline (Ward *et al.*, 2003).

Most of the southern margin of the ice sheet abutted water, tundra, or cold grassland. Herb tundra is indicated at pollen sites close to the ice margin in New Jersey (Sirkin *et al.*, 1970), including a site on a mountain nunatak (Cotter *et al.*, 1984). Macrofossils of arctic avens (*Dryas integrifolia*), arctic blueberry (*Vaccinium uliginosum*), alpine bistort (*Polygonum viviparum*), and the dwarf willows (*Salix arctica* and *S. herbacea*) – all common in modern herb tundra – are dated at 18.7 ka BP at a site in Minnesota (Baker *et al.*, 1999). A pollen sequence from an ice-marginal site in Ohio indicates forest tundra with spruce at 18 ka BP (Heusser *et al.*, 2002). Forest tundra is also indicated by pollen sequences from Iowa (Szabo, 1980), Maryland (Maxwell and Davis, 1972), Delaware (Russell and Stanford, 2000), and Pennsylvania (Martin, 1958) at this time. The ice evidently pushed into forested areas, shearing off trees and overriding forest soil layers in its great mid-continental lobes. Wood recovered from such sites is typically spruce with occasional larch (Burns, 1958; Ruhe, 1969; Lowell



et al., 1990). Beetle assemblages of this age recovered from two sites along the Mississippi River in Missouri and Illinois are similar to those living today in the southern boreal forest of Ontario, whereas beetle assemblages from sites closer to the ice sheet indicate forest tundra and tundra conditions (Schwert *et al.*, 1997). A boreal forest, dominated by spruce but with an admixture of limber pine (*Pinus flexilis*) of Cordilleran origin, evidently extended across the eastern Great Plains as far west as central Kansas, as suggested by both pollen and macrofossil evidence (Gruger, 1973; Wells and Stewart, 1987; May and Holen, 1993). The Cordilleran component is thought to have extended eastward through gallery forests along rivers.

At 18 ka BP, the Great Basin area of the American Southwest was substantially wetter than it is today, as indicated by the large pluvial lakes Bonneville and Lahontan that occupied now-dry basins (Oviatt *et al.*, 1992). Subalpine forest or subalpine parkland with bristlecone pine (*Pinus longaeva*), limber pine, and Engelmann spruce (*Picea engelmanii*), which today are limited to isolated mountain blocks within the Great Basin, along with mammals such as the pika (*Ochotona princeps*) that are adapted to conifer forest or parklands, occupied areas of present-day steppe and desert and adjacent mountains (Betancourt *et al.*, 1990; Madsen *et al.*, 2001). This greater moisture, which persisted until about 13 ka BP, has been explained as the result of the southward-displaced jet stream (COHMAP Members, 1988). However, sagebrush (*Artemisia* spp.) steppe persisted in the northern part of the Great Basin and vicinity (Barnosky, 1985; Mehringer, 1985), where the anticyclonic easterly winds prevailed. Phytolith evidence from loess sections reveals the presence of altitudinally arranged steppe with sagebrush (*Artemisia*) and a variety of

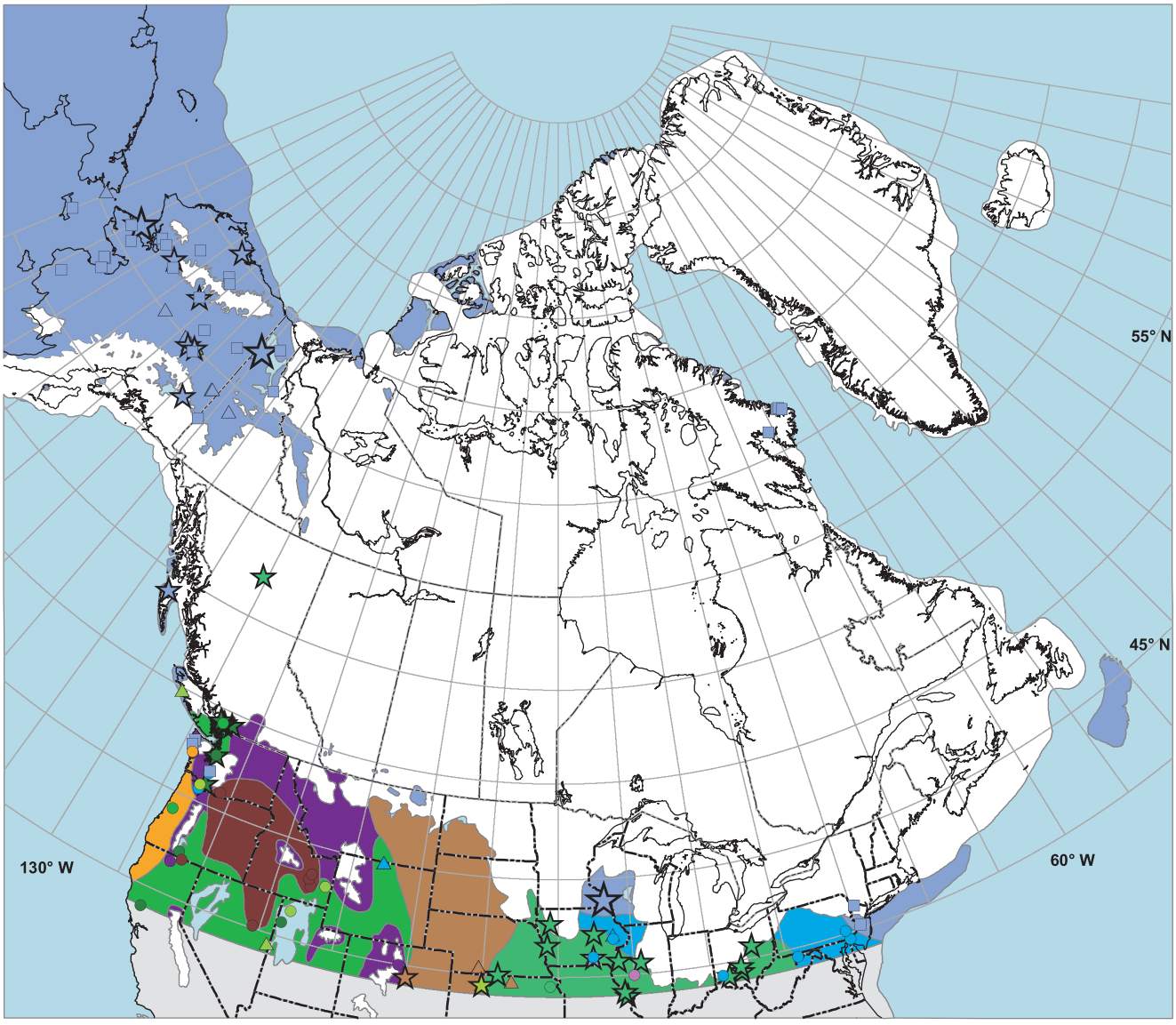


FIGURE 1. Biomes at 18 ka BP. The legend is common to all subsequent biome maps.

Les biomes en 18 ka BP. La légende est la même pour les cartes de biomes suivantes.

grasses (*Stipa* spp., *Poa* spp. and *Festuca* spp.), grassland dominated by *Poa* spp. and *Festuca* spp., conifer parkland with fir and spruce, and finally *Artemisia* steppe, proceeding from the Columbia River valley to the summit of the Blue Mountains in southeastern Washington (Blinnikov *et al.*, 2002). Treeline in the mountains of the Yellowstone region northeast of the Great Basin and in the Front Range of Colorado was about 500-600 m lower than present and alpine tundra was thus much more extensive than it is today (Baker, 1976; Legg and Baker, 1980). Treeline was presumably still lower farther to the north, thus allowing alpine tundra to extend down slope to the level of the northern Great Basin and the Great Plains closer to the ice sheet in Montana.

There is too little paleobotanical information to know with certainty whether the western plains were covered by grassland or by tundra at the last glacial maximum. Jackson *et al.* (2000) showed tundra in eastern Texas at this time based on pollen data, which presumably would imply tundra farther north on the plains as well. However, grassland beetles of this age occur in Colorado (Elias and Toolin, 1990) and the fairly widespread occurrence of grassland mammals (Table II; Graham *et al.*, 1987) is more suggestive of grassland than of herb tundra. Opal phytolith evidence points to grassland in southwestern South Dakota by 14 ka BP (Fredlund and Tieszen, 1997), when the regional climate was probably similar to that at 18 ka BP if similar ice-marginal positions are indicative of climate.

It is generally recognized that plant assemblages within all of the biomes at 18 ka BP lack close modern analogues. Thus, although spruce and its familiar associates such as larch and fir may have been abundant in the boreal forest at that time, in some places they occurred in association with elements such as elm, ash, and oak, which are more demanding of warmth. The mammal assemblages were also greatly different from those of today, not only by virtue of the fact that they included many extinct species (Tables II-III), but also because animals that now occupy separate ranges then occurred in association. These different-from-present associations, even if we consider only extant taxa, are usually referred to as "disharmonious" (Baker *et al.*, 1986). However, this term is somewhat misleading, because the disharmony amongst the animals or between the animals and their habitats was not necessarily greater than it is today. It is only since the middle Holocene, by which time migration rates had declined, that very close modern analogues can be found for the plant and animal assemblages. This recent marshalling of modern assemblages is believed to be partly a consequence of the fact that many northern biomes now occupy regions that differ fundamentally

TABLE II

The most common fossil mammals from sites south of the ice sheets during the interval of near maximum continental ice cover. The values here and in subsequent similar tables are the numbers of radiocarbon-dated occurrences north of 39 °N in the current database. The numbers include directly dated occurrences and occurrences that are associated with the dated material. Extinct and (or) extirpated taxa are marked with an asterisk

Mammal	25-20 ka	19.9-18 ka	17.9-16 ka	15.9-13 ka
A. Steppe, Grassland and Savannah				
Mammoth* (*Mammuthus* spp., *M. jeffersonii, M. columbi, M. imperator*)	15	4	5	8
Camel* (*Camelops hesternus*)	9		2	1
Bison *(Bison* spp., *B. latifrons*, B. crassicornis*, B. occidentalis**)	7	1		
Horse* (*Equus* spp., *E. conversidens*)	6		1	1
Prairie dog *(Cynomys* spp., *C. niobrarius*)	5	1	1	
Ground squirrel (*Spermophilus* spp., *S. parryii, S. richardsonii*)	4	1	1	1
Pocket gopher (*Geomys bursarius*)	3	1	1	
B. Wooded and Tundra areas				
Mammoth* *(Mammuthus* spp., *M. primigenius, M. columbi*)	3		1	3
Mastodon* (*Mammut americanum*)				10
Woodland muskox* (*Bootherium bombifrons*)	2		2	5
Elk-moose* (*Cervalces scotti*)				5
Caribou (*Rangifer tarandus*)			1	5
Short-faced bear* (*Arctodus simus*)	2		2	2
Dire wolf* (*Canis dirus*)	2		1	2
Wolf (*Canis lupus*)	2		1	1
Ground squirrel *(Spermophilus* spp., *S. parryii, S. richardsonii, S. tridecemlineatus*)	5	1	2	9
Bog lemming *(Synaptomys* spp., *S. borealis, S. cooperi*)	2		2	5
Tundra lemming *(Dicrostonyx* spp., *D. torquatus*)	6	1	6	3
Vole *(Microtus* spp., *M. miurus, M. montanus, M. pennsylvanicus, M. townsendii, M. xanthognathus*)	10	3	18	19

in radiation, seasonality, and daylight regimes from those previously occupied, and partly the result of the differing abilities of individual plant species to shift their ranges in response to climate change. Hence, one may either view sub-recent to ancient biome compositions as differing from "normal" and "harmonious" modern biomes, or one may view modern biome compositions as the rather arbitrary and transient results of displacements during the twenty or so glacial-interglacial cycles of the Quaternary.

From pollen data alone, a plant community dominated by grass (Gramineae), sage (*Artemisia* spp.), and sedge (Cyperaceae) occupied Beringia at 18 ka BP. Palynologists usually interpret this assemblage as representing herb tundra (Rampton, 1971; Matthews, 1974a, 1974b; Colinvaux, 1981; Cwynar, 1982; Ager and Brubaker, 1985; P. Anderson, 1985, 1988; P. Anderson *et al.*, 1988; Eisner and Colinvaux, 1990; Edwards and Baker, 1994; Ager, 2003). Survival of small populations of spruce (probably white spruce), poplar and tree birch in eastern Beringia is possible based on the pollen record (Brubaker *et al.*, 2005). Plant macrofossils of full-glacial age recovered from Beringian sites are typical tundra plants (Goetcheus and Birks, 2001; Zazula, 2003) representing a variety of soil moisture conditions, with willow being the only identified wood. Nevertheless, numerous large mammal fossils, especially of woolly mammoth (*Mammuthus primigenius*), Yukon horse (*Equus lambei*), and steppe bison (*Bison priscus*), indicate that this biome was sufficiently productive to support herds of these grazers (Table III; Burke and Cinq-Mars, 1996; Guthrie, 2003, 2006). In contrast, modern tundra can support only caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*), neither of which relies on grass. For this reason, vertebrate paleontologists have proposed that eastern Beringia then supported a biome, termed "steppe tundra" or "mammoth steppe", which has no modern biome-level analogue (Guthrie, 2001). Use of the term herb tundra herein is not meant to convey a pervasively wet soil condition nor a biome too unproductive to support the large grazers that evidently lived there. Nevertheless, in much of the High Arctic today, plant cover is more limited by moisture and nutrient availability than by temperature (Edlund, 1992).

The so-called productivity paradox of full glacial Beringia may have been resolved by the analysis of Zimov *et al.* (1995). They proposed that the change from a more grass-dominated tundra (or steppe) of full-glacial Beringia to the moss-sedge-dominated tundra of postglacial time is the result of megaherbivore extinction, rather than of climate change. Essentially, hoof trampling and grubbing militates against survival of fragile mosses, whereas grasses are not only resistant to trampling because they are deep rooted but also because they transpire much more water and thus reduce soil moisture, further promoting grasses over mosses and wet-ground sedges. Grass survival was also favoured, and moss survival disadvantaged, by widespread loess accumulation, as was characteristic of eastern Beringia (Péwé, 1975). Abundant grasses, being nearly an order of magnitude more nutritious and being less chemically defended from grazing than tundra sedges, ensured the viability of grazing herds. In this view, both Beringian megaherbivore extinction and postglacial tundra evolution resulted from overkill by Paleoindians and Holocene sedge-moss-willow tundra may be seen as a geologically unique anthropogenic biome. Zimov's hypothesis is a reason to apply caution in seeing all Late Wisconsinan botanical changes as being strictly climate forced. On the other hand, only the most general support for it can be drawn presently from the Beringian archaeological record (West, 1996; Dixon, 2001; Yesner, 2001; Guthrie, 2006).

14 ka BP

Although some ice-marginal recession had occurred in the southeast, the ice sheets at 14 ka BP were still in near maxi-

TABLE III

The most common fossil mammals of Beringia during the interval of near maximum continental ice cover. Extinct or extirpated taxa are marked with an asterisk

Mammal	25-20 ka	19.9-18 ka	17.9-16 ka	15.9-13 ka
Horse* (*Equus* spp., *E. lambei*)	33	28	11	24
Bison* *(Bison* spp., *B. priscus*)	20	7	5	12
Mammoth* *(Mammuthus* spp., *M. primigenius*)	32	24	16	50
Saiga antelope* (*Saiga tatarica*)			1	3
Woodland muskox* (*Bootherium bombifrons*)	3		2	
Tundra muskox (*Ovibos moschatus*)	1		1	2
Caribou *(Rangifer* spp.)	7		1	3
Dall sheep (*Ovis dalli*)	4			3
Short-faced bear* (*Arctodus simus*)	4			
American lion* (*Panthera atrox*)	2			1
Wolf (*Canis lupus*)	2	1	1	
Grizzly bear (*Ursus arctos*)	2	2		11
Ground squirrel (Spermophilus spp., *S. parryii*)	11	2	2	8
Lemming (*Dicrostonyx torquatus*)	3		1	1

mal configurations (Fig. 2). Indeed, parts of the southwestern ice margin were at their most advanced positions, specifically in Washington State, South Dakota, and Iowa. The ice lobe in Iowa overrode ground supporting spruce, larch, and hemlock at this time (Ruhe, 1969, 1983; Bettis *et al.*, 1996). The ice lobe in the Puget Sound of Washington displaced Sitka spruce (Porter and Swanson, 1998) and cedar re-invaded quickly after ice recession by 13.6 ka BP (Porter and Carson, 1971). Both these advances are indicated by dated wood and they suggest that the ice contacted a forest similar to the northern part of the present coast forest.

Despite these ice advances in the southwest, warming is indicated in the southeastern periglacial region. The boreal forest, forest tundra, and shrub tundra (Spear and Miller, 1976; Watts, 1979; Gaudreau and Webb, 1985) had advanced northward in the mid-continent to New England region. Newly formed ice-marginal herb tundra was dominated by sedge everywhere from Minnesota eastward. The shrub tundra along the Atlantic seaboard was dominated by shrub birch everywhere except in the south, where alder (*Alnus* spp.) and juniper (*Juniperus* spp.) were the most common shrubs. Spruce was the chief tree component of forest tundra, boreal forest, and boreal parkland at all sites known from this time; the main reported associate trees were fir (probably *Abies balsamea*), jackpine, birch (probably *Betula papyrifera*), larch, alder, and ash. Warming is also indicated by the development of a mixed forest of blue oak (*Quercus douglasii*) and digger pine (*Pinus sabiniana*) with Douglas fir (*Pseudotsuga menziesii*) in the coastal range of California before 14 ka BP (Adam *et al.*, 1981).

Development of shrub tundra with dwarf birch (*Betula glandulosa*) in the Bering Strait lowlands of Beringia indicates warming there at 14 ka BP (Ager, 1983; Anderson, 1985; Elias

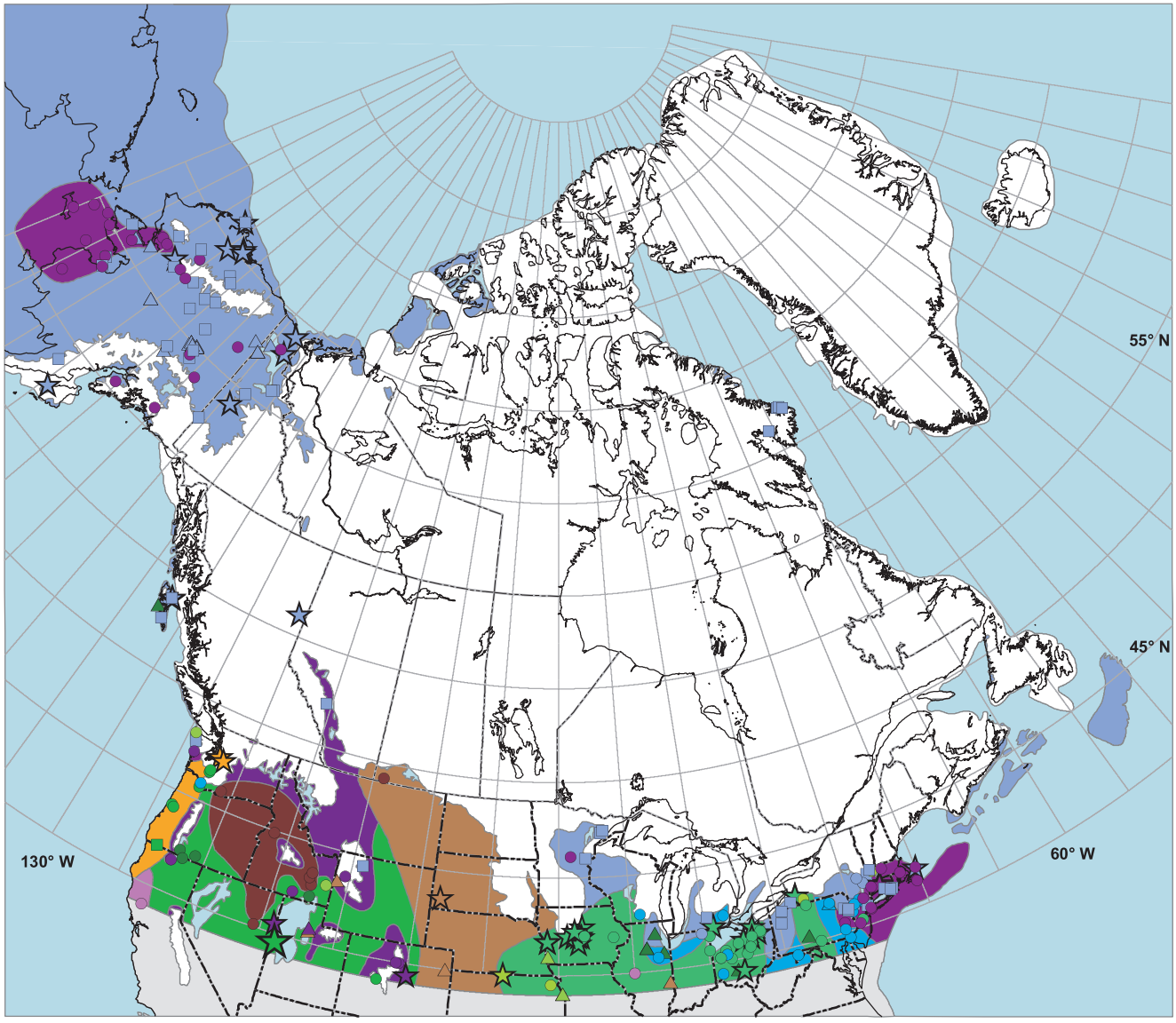


FIGURE 2. Biomes at 14 ka BP. *Les biomes en 14 ka BP.*

et al., 1996). Guthrie (2001) has proposed that this lowest part of eastern Beringia hosted a moister vegetation assemblage throughout the last glaciation, referring to the region as Beringia's "mesic buckle." Although it does not appear to have been warm enough to support shrub birch prior to 14 ka BP, it may have supported a more mesic herb tundra community, as opposed to steppe, at that time, as is required by the long-held concept that Beringia served as a major refugium from which mesic tundra plants dispersed during the postglacial (Hultén, 1937). Shrub tundra establishment indicates that warming and moistening occurred at high latitudes, not just at low latitudes, early in the process of global deglaciation. If dwarf birch did not survive the last glacial maximum in Beringia, it probably arrived at this time from Siberia. The three dominant grazers of eastern Beringia, horse, bison and mammoth, remained abundant (Table III; Guthrie, 2006).

EARLY DEGLACIATION (13-11 KA BP)

This period starts with the onset of more rapid recession of southern ice margins and ends with the onset of the Younger Dryas cold interval.

13 ka BP

By this time, herb tundra had been nearly eliminated in the southeast (Fig. 3). As before, the few sites representing herb tundra from Minnesota eastward were dominated by sedge. Sage dominated the newly formed herb tundra in Alberta, thus indicating drier conditions there (Mott and Jackson, 1982 [chronology adjusted]; Hickman and Schweger, 1991, 1993; Beaudoin *et al.*, 1996; Mandryk, 1996). The sage could have spread from either the grassland or the alpine tundra to the south, and indeed a distinction of herb tundra from periglacial

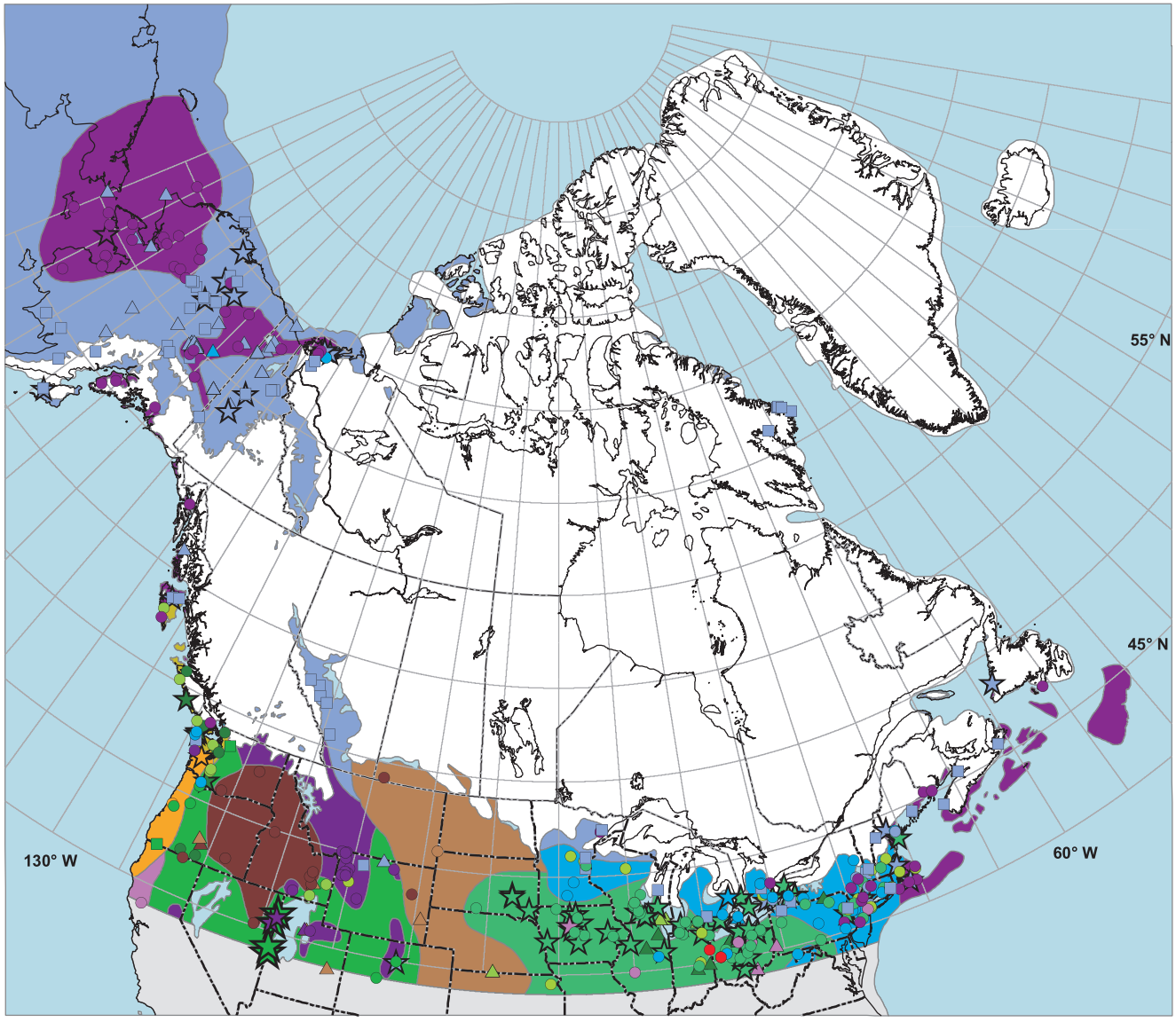


FIGURE 3. Biomes at 13 ka BP. *Les biomes en 13 ka BP.*

grassland is perhaps meaningless here. Shrub tundra with dwarf birch, juniper, and willow had spread into Atlantic Canada as far as southern Newfoundland (Mott, 1975; Mayle *et al*., 1993; Anderson and Macpherson, 1994). Macrofossils of *Salix herbacea* and *Dryas* spp. – important plants in the modern tundra – have been directly dated to 13.15 ka BP from a site in Maine (Thompson *et al*., 1999; Ridge *et al*., 1999). As earlier, this biome included alder at warmer sites in New York and Massachusetts (Ogden, 1963; Ibe, 1982; Maenza-Gmelch, 1997a, 1997b).

The expansion of forest tundra to the ice margin in central and eastern U.S.A. and southern Ontario left little room for herb tundra. Tundra plants – *Salix herbacea, Dryas integrifolia*, and *Vaccinium uliginosum* – and forest tundra assemblages of beetles dating just prior to this time are reported from a site near the ice margin in Michigan (Morgan, 1987). Closeness of spruce to the ice margin in Ontario is demonstrated by the presence in till of wood dated at 13.1 ka BP (Gravenor and Stupavsky, 1976). Similarly, white spruce cones dated at 12.51 ka BP have been recovered from glaciomarine sediment in Maine (R. Anderson *et al*., 1990) indicating the presence of forest tundra (if not forest) close to the ice margin. Meanwhile the boreal forest expanded into newly deglaciated terrain in the southern Great Lakes region and into tundra farther east (Winn, 1977; Davis and Jacobson, 1985; Schwert *et al*., 1985; Thorson and Webb, 1991; Morris *et al*., 1993; Peteet *et al*., 1994; Winkler and Sanford, 1995). This forest expansion brought with it, presumably from areas farther south, the spruce-browsing mastodon (*Mammut americanum*), whose population appears to have increased markedly north of 39° N after 14 ka BP (Tables II and IV). Spruce was the most abundant tree at most sites in the forest tundra, with jackpine appearing in Pennsylvania, *Populus* in Maine, and ash in Michigan; black ash extends into the southern boreal forest of eastern Canada today. Similarly, spruce continued to dominate at boreal forest sites, with fir as adjunct at nearly

TABLE IV

The most common fossil mammals south and west of the ice sheets at 12.9-10 ka BP. Extinct or extirpated taxa are marked with an asterisk

Mammal	12.9-12 ka	11.9-11 ka	10.9-10 ka
A. Steppe, Grassland and Savannah			
Mammoth* *(Mammuthus* spp., *M. columbi, M. jeffersonii, M. primigenius*)	11	18	23
Horse* *(Equus* spp., *E. conversidens*)	2	6	9
Bison *(Bison* spp., *B. antiquus*, B. occidentalis**)	4	20	55
Camel* (*Camelops hesternus*)	3	9	4
Pronghorn (*Antilocapra americana*)	2	4	8
Dire wolf* (*Canis dirus*)	2		2
Short-faced bear* (*Arctodus simus*)	1	3	1
Ground squirrel *(Spermophilus* spp., *S. lateralis, S. richardsonii, S. tridecemlineatus*)	2		14
B. Forest tundra, Alpine tundra and Tundra			
Caribou (*Rangifer tarandus*)	3	4	8
Peccary* *(Platygonus* spp., *Mylohyus* spp.)	3	1	
Bighorn sheep (*Ovis canadensis, O.c. catclawensis**)	1	3	9
Grizzly bear (*Ursus arctos*)	1	5	3
Lemming *(Dicrostonyx* spp.)	1	1	3
C. Conifer Forest and Conifer Parkland			
Mastodon* (*Mammut americanum*)	14	27	31
Mammoth* *(Mammuthus* spp., *M. columbi, M. jeffersonii, M. primigenius*)	23	2	2
Elk-moose* (*Cervalces scotti*)	6	15	5
Woodland muskox* (*Bootherium bombifrons, Symbos* spp.)	1	2	1
Bison *(Bison* spp., *B. antiquus*, B. occidentalis**)	2	7	20
Caribou (*Rangifer tarandus*)	2	4	10
Elk *(Cervus* spp., *C. elaphus*)	1	2	5
Deer (*Odocoileus* spp., *O. virginianus*)	2	8	4
Giant beaver* (*Castoroides ohioensis*)	1	5	11
Beaver (*Castor canadensis*)	7	12	21
Muskrat (*Ondatra zibethicus*)	7	11	17
Bear (*Ursus americanus*)		6	18
Vole *(Microtus* spp., *M. pennsylvanicus, M. xanthognathus*)	10	17	27

half of sites, but spread throughout the extent of the biome. Larch and ash, as components of the boreal forest, seem to have been concentrated in the mid-continent.

Birch shrub tundra had expanded greatly in Beringia by 13 ka BP (Matthews, 1974b; Ager, 1982; Heusser, 1983; P. Anderson, 1988; Eisner and Colinvaux, 1992; Oswald *et al.*, 1999), but it was still somewhat less extensive than herb tundra. This shrub expansion at the expense of grass, sedge, and sage does not seem to have led to great reduction in the numbers of the large grazing animals (Tables III and V). It may account for a further reduction in the size of Alaskan horses. However, that process was under way by 25 ka BP, at the beginning of the Late Wisconsinan cold stage and prior to both the last glacial maximum and birch expansion (Guthrie, 2003). Numbers of bison appear to have been increasing at this time, which Guthrie (2006) attributes to an increase in availability of willow forage.

A forest, with lodgepole pine and mountain hemlock as vanguards, advanced northward along the Pacific coast very soon after local deglaciation, reaching the Queen Charlotte Islands by 13 ka BP (Hebda, 1983, 1995, 1997; Brown and Hebda, 2002). Coastal shrub tundra occupied the narrow strip of ice-free land from the Queen Charlottes to Cook Inlet in Alaska (Rymer and Sim, 1980; Sirkin and Tuthill, 1987; Mathewes *et al.*, 1993; Hebda, 1995; Hansen and Engstrom, 1996). Conditions in the American Southwest remained similar to those at 14 ka BP.

12 ka BP

It is possible that by 12 ka BP herb tundra was expanding northward from the easternmost parts of the Beringian refugium on Banks, Prince Patrick, and Melville islands (Fig. 4). A sample containing mainly moss and lichen, but with some willow (*Salix arctica*), from Ellef Ringnes Island was dated at 11.8 ka BP, but subsequent redating failed to confirm this antiquity (D.A. Hodgson in McNeely, 1989; D.A. Hodgson, personal communication, 2004). This site was probably deglaciated shortly after 12 ka BP. If the willow component of the sample truly dates to this time, the site was warmer than it is presently and mean July temperatures were above 3 °C, because the site is beyond the present limit of willow (Edlund and Alt, 1989).

At 12 ka BP, eastern Beringia was entirely covered by birch-willow shrub tundra except in the cold fringe along the Arctic Ocean and in alpine and periglacial areas, where herb tundra remained (Brubaker *et al.*, 1983; Edwards *et al.*, 1985; Edwards and Brubaker, 1986; Billings, 1987; Lozhkin *et al.*, 2001). However, bison, mammoth, saiga antelope (*Saiga tatarica*), and possibly horse continued to occupy this area, indicating that grasses and other herbs were still sufficiently abundant to support them (Table V). Of these four extinct Beringian large mammals, however, only bison would continue to occupy the region for long after 12 ka BP, perhaps indicating that self-maintenance of the steppe tundra by herbivores had declined to a critical point (see above and Zimov *et al.*, 1995). Alternatively, herb reduction due to competition, winter snow depth, or icing events due to winter rainfalls were then becoming critical in limiting access to forage. The saiga antelope is particularly intolerant of snow deeper than 20 cm and of wet ground (Harington and Cinq-Mars, 1995). The most remarkable change in Beringian biome composition was the sudden appearance of elk (*Cervus elaphus*) shortly after 13 ka BP and their great population expansion about 12.5 ka BP, when the first moose (*Alces alces*) also may have arrived in the region (Guthrie, 2006). Moose are not common in tundra areas today and in Beringia they may have relied on browsing of willow and dwarf birch. Guthrie (2006) suggested that both elk and moose might have arrived in eastern Beringia at this time along with humans from Eurasia. This suggestion is supported by the absence of direct dates on these taxa south of the ice sheets prior to 10 ka BP. Note, however, that *Cervus* has been associated with radiocarbon dates on charcoal of 13.2-19.6 ka at a site in Pennsylvania (Adovasio, 1977).

By 12 ka BP, an ice-free corridor had opened between the Cordilleran and Laurentide ice sheets, with herb tundra in its

TABLE V

The most common fossil mammals in Beringia at 12.9-10 ka BP. Extinct or extirpated taxa are marked with an asterisk

Mammal	12.9-12 ka	11.9-11 ka	10.9-10 ka
A. Tundra			
Mammoth* *(Mammuthus* spp.)	17	6	
Bison* *(Bison* spp., *B. priscus*)	20	18	8
Horse* *(Equus* spp., *E. ferus/caballus, E. lambei*)	9	1	
Saiga antelope* (*Saiga tatarica*)	4		
Dall sheep (*Ovis dalli*)	1	9	4
Grizzly bear (*Ursus arctos*)	3	1	1
Ground squirrel *(Spermophilus* spp., *S. parryii*)	3	11	3
B. Forest Tundra			
Caribou (*Rangifer tarandus*)	3	9	3
Elk (*Cervus elaphus*)	47	14	11
Moose (*Alces alces*)	2	19	9
Beaver (*Castor canadensis*)		1	

northern part (Szeicz *et al.*, 1995), birch shrub tundra in its southern part (White *et al.*, 1985; Mandryk, 1996), and grassland still farther south (Klassen, 1994). Meanwhile, shrub tundra had extended into newly deglaciated parts of New England and Atlantic Canada. Amongst the dwarf trees, this biome was characterized by birch and willow throughout, though juniper occurred as far north as Newfoundland, alder was established in Nova Scotia, and soapberry (*Shepherdia canadensis*) was present in New Hampshire. Forest tundra extended through parts of that region that were deglaciated earlier, reaching southwestern New Brunswick (Whitehead *et al.*, 1989; Spear *et al.*, 1994; Jetté and Mott, 1995; Miller and Elias, 2000). Plant macrofossils from glacial lake sediments in Vermont dating at 12.35 ka BP reveal the presence of diverse arctic-alpine plants that must have contributed to the forest tundra understory. These include willows (*Salix herbacea* and *S. reticulata*), arctic avens, moss campion (*Silene acaulis* and *S. involucrata*), mountain sorrel (*Oxyria digyna*), saxifrages (*Saxifraga oppositifolia* and *S. aizoides*), and arctic blueberry. Several of these survive as relicts today in patches of tundra on the Appalachian Mountains (Miller and Spear, 1999). Amongst the trees, spruce appears to have been the most abundant in the western part of the biome, giving way to poplar and birch in the more oceanic regions of Maine and New Brunswick. By 12 ka BP, maximum lake surface temperatures, as inferred from chironomids, close to the residual ice cap in the shrub tundra of coastal southwestern Nova Scotia, were about 18 °C (Wilson *et al.*, 1993), implying a mean July air temperature of about 14 °C (I. Walker, personal communication, 2004), which is certainly capable of supporting forest. Similarly, July air temperatures inferred from fossil beetles at several sites in Nova Scotia and New Brunswick had risen to within 2-4 °C of modern values by 12 ka BP, whereas winter temperatures were 12-13 °C colder than present (Miller and Elias, 2000).

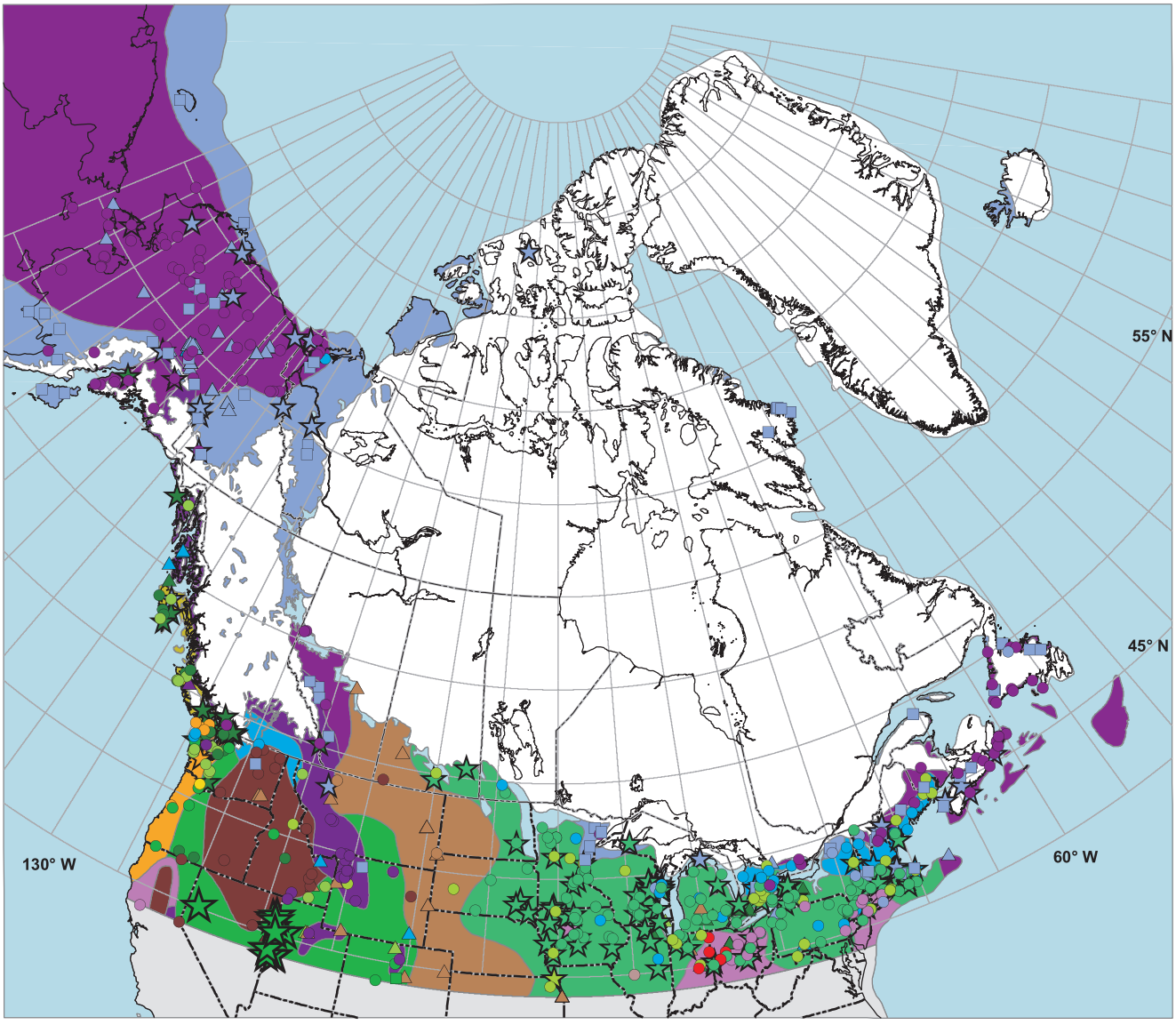


FIGURE 4. Biomes at 12 ka BP. *Les biomes en 12 ka BP.*

At 12 ka BP, boreal forest and forest tundra fringed most of the southern margin of the ice sheet, with forest forming a great belt extending from south-central Saskatchewan (Ritchie and deVries, 1964; Terasmae, 1973) and Kansas (Watts, 1983) to the Atlantic Ocean (Newby *et al.*, 2000; Shuman *et al.*, 2001) and occupying vast areas that are today grassland. As before, spruce was the most abundant tree at most sites, though jackpine had come to prominence in parts of New York and Pennsylvania. Larch and ash were common in areas of Minnesota, Iowa, Wisconsin, Illinois and Indiana. Fir was widespread, except perhaps in Minnesota and regions north and west of there. The mastodon evidently continued its expansion in this biome (Table IV), probably most abundant amongst the large mammals (note that the larger number on dates associated with *Mammuthus* are due to multiple datings at a single site). Elk-moose (*Cervalces scotti*) and woodland muskoxen (*Bootherium bombifrons*) also occupied the coniferous forest, while mammoths (*Mammuthus jeffersonii, M. columbi, M. primigenius*) and bison occupied forest openings and areas of boreal parkland.

Mixed forest had expanded northward nearly to Lake Erie (Shane, 1987, 1989; Shane and Anderson, 1993) and into southern New England (Peteet *et al.*, 1994; Maenza-Gmelch, 1997a, 1997b). At most sites this forest retained substantial amounts of spruce and (or) pine (probably white pine), but ash, ironwood, elm, oak, and – in the east – beech were significant components. Indications of deciduous forest in Ohio and Indiana at this time may suggest very early establishment of more thermophilous vegetation at favourable sites or, more probably, problems with radiocarbon dating in this hardwater region (Shane, 1987; Shane and Anderson, 1993).

Steppe, still dominated by sagebrush, had expanded in the Great Basin and Death Valley of the American Southwest (Adam, 1967; Mehringer, 1977) and northward to the Canadian border, where grass and sedge were also significant components and scattered pines occurred (Mack *et al.*, 1978). However, subalpine forest remained the dominant biome of the Cordilleran region (Mack *et al.*, 1978, 1979; Thompson and Mead, 1982; Wells, 1983; Thompson *et al.*, 1986; Rhode and Madsen, 1995). This was primarily a spruce-pine forest in the Rocky Mountains (Vierling, 1998; Doerner and Carrara, 2001) and a spruce-pine-subalpine fir-mountain hemlock-alder forest in the wetter ranges west of the Great Basin (Barnosky, 1985; McLachlan and Brubaker, 1994; Sea and Whitlock, 1995). Within the Great Basin, bristlecone pine, limber pine, and junipers were the main trees. Sitka spruce was probably more important in the wetter regions west of the basin and Engelmann spruce inland.

The forest along the Pacific coast at 12 ka BP was still dominated in the north by early successional trees such as lodgepole pine, mountain hemlock, and alder. Lodgepole pine had reached at least 58.4 °N (Mann, 1986). However, Sitka spruce, a dominant of the modern northern section of the coast forest, had reached the Queen Charlotte Islands by this time (Hebda, 1995), western hemlock had reached southern Vancouver Island (Brown and Hebda, 2002) and Ponderosa pine (*Pinus ponderosa*) had reached nearly 49 °N in Washington (GSC-4939). The grizzly bear expanded through the coast forest-alpine tundra complex to the Alaska Panhandle by 12.3 ka BP (Heaton *et al.*, 1996), possibly from Beringia where it was common earlier (Barnes *et al.*, 2002), and the mountain goat (*Oreamnos americanus*) reached the mountain ridges of Vancouver Island by 12.2 ka BP (Nagorsen and Keddie, 2000).

11 ka BP

Birch shrub tundra continued to dominate the Alaska to Mackenzie Delta region, which was newly separated from Siberia by submergence of Bering Strait (Fig. 5). The incipient appearance of patches of forest tundra in that region, with the only tree evidently being aspen or poplar (*Populus* spp.; provided that none of the birch pollen is from tree birch), is indicated both by pollen records (Ager, 1983; Brubaker *et al.*, 1983; Spear, 1983; P. Anderson, 1988; Spear, 1993; Hu *et al.*, 1996) and by a few wood macrofossil sites, including one that indicates the presence of beaver (*Castor canadensis*) (Hopkins *et al.*, 1981; West, 1981). Being so far from the main continental treelines at that time, these forest patches invite speculation that birds, arriving either from Siberia or North America, dispersed the poplar seeds, though expansion from cryptic refugia within Beringia has also been proposed (Brubaker *et al.*, 2005). Nevertheless, this date places the beaver in an odd environmental context (again provided that none of the birch pollen is from local tree birch), because this animal's range does not extend beyond latitudinal treeline today (Banfield, 1977). Two of the wood macrofossil sites are north of the present poplar range, which suggests that the climate of Alaska was then warmer than present (Kaufman *et al.*, 2004). Alternatively, both the lake sediment and wood dates may be erroneously old (the oldest poplar date has a large standard error: 11 800 ± 750 (UCLA-1859)) and poplar arrival may date closer to 10 ka BP. As mentioned, mammoth and horse had probably disappeared from Beringia by 11 ka BP, perhaps because of the wetter tundra conditions (Zimov *et al.*, 1995). Alternatively, they may have succumbed to the newly arrived Paleoindian hunters, who had moved into the area by 11.7 ka BP or earlier (Yesner, 2001), though direct evidence of this cause is lacking. However, Guthrie (2003) argued that horses were extinct in Alaska by 12.5 ka BP, before the earliest proven (or currently accepted) arrival of man, and that extinction may have been brought about by the same pressures that caused the body-size reduction of the horses over the preceding millennia. Whatever the cause, this regional extinction left bison, elk, moose, caribou and Dall sheep (*Ovis dalli*) prominent among the large grazers and browsers, along with the omnivorous grizzly bear.

Recently deglaciated parts of Atlantic Canada, Québec, and Maine by this time were occupied by herb tundra, shrub tundra, and forest tundra in succession outward from the ice sheet margin (Terasmae, 1973; Richard and Poulin, 1976; Mott, 1977; Richard, 1977; Savoie and Richard, 1979; Green, 1981; Mott and Farley-Gill, 1981; Walker and Paterson, 1983; Tolonen and Tolonen, 1984; Macpherson, 1985; Mott *et al.*, 1986; Dredge *et al.*, 1992; Jetté and Richard, 1992; Mayle *et al.*, 1993; Wolfe and Butler, 1994; McCarthy *et al.*, 1995; Marcoux and Richard, 1995; Jetté and Mott, 1995). In

Newfoundland, eight sites reverted from shrub tundra to herb tundra by about 11 ka BP (T. Anderson and Lewis, 1992; T. Anderson and Macpherson, 1994) and remaining shrub tundra was characterized by birch and willow amongst the shrubs. Birch and willow were also the most important shrubs west of the Gulf of St. Lawrence, but alder also survived there. Macrofossil records for this time include arctic avens in herb tundra of western Newfoundland (GSC-1350), willow (*Salix herbacea*), arctic avens, mountain sorrel, moss campion, and bladder campion (*Melandrium affine*) in the shrub tundra of Québec (Mott *et al.*, 1981; Govare and Gangloff, 1989), and *Salix herbacea* in Vermont (Miller and Spear, 1999). Despite that impoverished plant cover prior to the onset of Younger Dryas cooling, the maximum summer surface temperatures of small lakes in Maine, southern New Brunswick, and southwestern Nova Scotia – as indicated by chironomids – had already risen to modern levels (20-25 °C; Wilson *et al.*, 1993; Levesque *et al.*, 1997). Insect remains similarly indicate attainment of modern summer temperatures by 11 ka BP (Miller and Elias, 2000). These temperatures are sufficient to support a mixed forest, and they were as high as those experienced during the post-Younger Dryas interval of forest cover. Presumably, therefore, the lack of extensive forest cover at 11 ka BP was due to inadequate migration time in tundra areas and inadequate forest densification time in areas of forest tundra. Farther west in New Hampshire, where lowland sites were already covered with boreal forest at 11 ka BP (sites presently in mixed forest), maximum lake surface temperatures had risen to about 18 °C (Cwynar and Spear, 2001).

The boreal forest at 11 ka BP extended from eastern Alberta (Schweger, 1989) and the Dakotas (McAndrews *et al.*, 1967; Watts and Bright, 1968; Radle *et al.*, 1989; Laird *et al.*, 1996) to the Atlantic Ocean, reaching the ice margin from the Ottawa Valley westward (Anderson, 1985). A partial tree

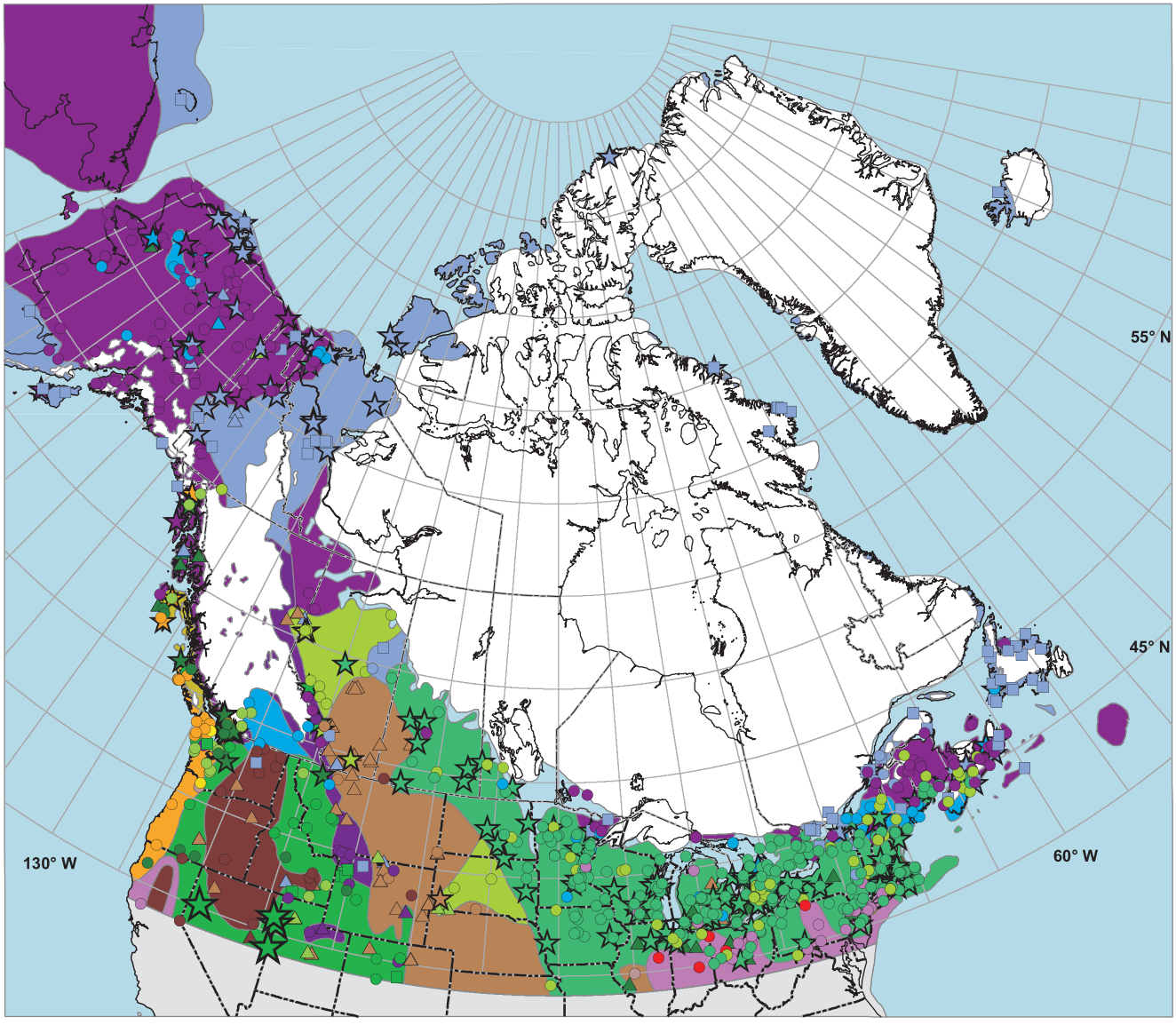


FIGURE 5. Biomes at 11 ka BP. *Les biomes en 11 ka BP.*

cover mainly of poplar with spruce and birch extended westward through a boreal parkland to the mountain front in northern Alberta (Lichti-Federovich, 1972; White *et al.*, 1979; Vance *et al.*, 1983; Schweger, 1989; Hickman and Schweger, 1991). West of Minnesota, the boreal forest was characterized by spruce with poplar, juniper, or birch growing where the forest was more open. In Minnesota, Iowa, Wisconsin, Illinois, and Indiana, assemblages were more diverse. Although spruce was prevalent throughout this region, larch, fir, and ash were important along with birch and poplar. Spruce seems to have been the most common tree closest to the ice margin in Ontario and Michigan, while jackpine increased southward to characterize some sites in Pennsylvania. Assuming that radiocarbon-dated fossil abundance reflects population size, the mastodon continued its expansion in the boreal forest between 12 and 11 ka BP, as did the elk-moose, the second most commonly dated mammal fossil (Table IV). Alternatively, human hunting may have increased the numbers of animals dying or being cached at sites of good bone preservation, such as in small ponds and bogs, where finds of these fossils are typically located (Fisher, 1995). Paleoindians using fluted, lanceolate, projectile points had spread throughout most areas south of the ice sheets by 11 ka BP and possibly by 11.5 ka BP (Ellis *et al.*, 1998; Canadian Archaeological Radiocarbon Database, 2005). Many archaeological sites of this period, few of which are radiocarbon dated, are located on the relict shorelines of the glacial Great Lakes (Jackson, 1983). Spruce forests and parkland surrounded these sites; none are known from areas shown here as occupied by tundra.

To the south, mixed forest formed a latitudinal belt from Illinois to the Atlantic (Watts, 1979). It seems to have formed by migration of elm, ironwood, and oak into the fringe of the boreal forest of the mid-continent and by an increase in the abundance of the already established ash there, and by northward migration of white pine and oak into the boreal fringe in Pennsylvania and New York while established birch populations there expanded.

Open ground in the form of grassland and tundra extended from 39 °N across the western plains and through the northern Cordillera to Alaska, interrupted only by the boreal parkland in northern Alberta (Watts and Wright, 1966; Bradbury, 1980; MacDonald, 1982; Markgraf and Lennon, 1986; Klassen and Vreeken, 1987; Barnosky *et al.*, 1987). This interval probably offered the greatest opportunity for postglacial northward dispersal of southern herbs, as invoked by Strong and Hills (2003) to account for northern disjuncts of several species that occur in the region today as far north as Peace River, but whose main distribution extends no farther north than Montana. Mammoths (*Mammuthus columbi, M. jeffersonii*) and extinct forms of bison (*Bison occidentalis, B. antiquus*) were widespread on the grasslands along with horse (*Equus conversidens*), camel (*Camelops hesternus*), short-faced bear (*Arctodus simus*), and pronghorn (*Antilocapra americana*) (Table IV). The distribution of fluted projectile points in western Canada indicates that Paleoindians occupied these recently deglaciated landscapes (Jackson and Duk Rodkin, 1996).

The American Southwest remained substantially moister than today, but drier than during full-glacial times (references previously cited). By 11 ka BP, treeline had risen so that subalpine forest replaced alpine tundra at some sites, although alpine tundra remained in some areas. In Colorado, Wyoming, Montana, and Idaho, the subalpine forest was characterized by Engelmann spruce, subalpine fir, whitebark pine, lodgepole pine, and limber pine, with birch and alder in places (Mehringer *et al.*, 1977; Carrara, 1995; Fall *et al.*, 1995; Feiler *et al.*, 1997). Douglas fir had reached the Rocky Mountains of Montana as a minor component of the subalpine forest (Brant, 1980).

The coast forest seems to have changed little in extent between 12 and 11 ka BP, though lodgepole pine forest reverted to shrub tundra on the northern Queen Charlotte Islands and mountain hemlock was beginning a resurgence at lowland sites in lower British Columbia and Washington at the beginning of Younger Dryas time (Mathewes, 1993). Western hemlock, silver fir (*Abies amabilis*) and Douglas fir had reached Vancouver Island by 11 ka BP (Heusser, 1983; Hebda, 1997; Brown and Hebda, 2003). The Alaska Panhandle seems to have been mainly covered in shrub tundra with patches of herb tundra (Mann, 1983), although lodgepole pine had reached favourable sites near to 60 °N by 10.7 ka BP (Cwynar, 1990; Peteet, 1991) or even by about 12 ka BP (Hansen and Engstrom, 1996). Macrofossils place lodgepole pine at Glacier Bay (58.9 °N) and Pleasant Island (58.3 °N) by 10.9 ka BP, and spruce cones at Glacier Bay date to 11.1 ka BP (Goodwin, 1988). Thus, the true vegetation cover of southeastern Alaska at 11 ka BP may have been a mosaic of forest and tundra irresolvable at small scale. Temperatures were still about 3 °C below present in southwestern British Columbia at 11 ka BP (Walker and Pellatt, 2003).

MIDDLE DEGLACIATION (10.9-7.6 KA BP)

The beginning of this interval coincides with the onset of Younger Dryas cooling, which terminated about 10 ka BP. Several pollen stratigraphic studies have identified regional responses of vegetation to this cooling. Cooling was most pronounced in the Canadian Maritimes, where maximum lake-surface temperatures dropped by as much as 20 °C from pre-Younger Dryas levels (Levesque *et al.*, 1997) and where forest tundra reverted to shrub tundra and shrub tundra to herb tundra (Mott *et al.*, 1986; Mott and Stea, 1993). Younger Dryas cooling has also been recognized in the northeastern states (Peteet *et al.*, 1990), and in the mid-continent (Shane, 1987) from resurgences of the pollen of cold-tolerant trees such as spruce. Possible responses in British Columbia and Washington (Mathewes, 1993; Mathewes *et al.*, 1993) include a reversion from forest to tundra on part of the Queen Charlotte Islands and increases in cold-tolerant mountain hemlock in the Fraser Valley and on the Olympic Peninsula. In southeast Alaska the response resembles that on the Queen Charlotte Islands (Engstrom *et al.*, 1990), whereas in southwest Alaska birch shrub tundra reverted to herb tundra (Hu *et al.*, 1995). However, these Pacific region records of Younger Dryas cooling show a much less marked response than those around the North Atlantic. Unfortunately these responses are not fully captured at the coarse time resolution of the present map series and probably not by some of the pollen records. However, the remnant ice sheets responded by pausing or

re-advancing in many places, though without overall increase in area of ice cover (Dyke, 2004). The middle deglaciation interval ends with the deglaciation of Hudson Bay at 7.6 ka BP. It is thus an interval of still-large remnant ice sheets, large enough to strongly affect the continental climate and for the pace and pattern of deglaciation to largely dictate the pattern of plant colonization.

10 ka BP

By 10 ka BP, the herb tundra of the Canadian arctic islands was sufficiently rich to support muskoxen, which had advanced at least as far north as Banks Island by 10.6 ka BP or else had survived there throughout the last glacial maximum (Maher, 1968). Forest tundra, still involving mainly poplar species and possibly some tree birch and including sites north of the present range of poplar, had expanded greatly in the Alaska-Mackenzie region (Fig. 6; Colinvaux, 1981; Ritchie, 1984; Slater, 1985; Edwards and Brubaker, 1986; Anderson *et al.*, 1990; Cwynar and Spear, 1991; Keenan and Cwynar, 1992; Hu *et al.*, 1993; Edwards and Baker, 1994), which was otherwise occupied by birch shrub tundra. The northwestern forest tundra evidently remained unconnected to the continental forest cover. This disjunct distribution may indicate that it is here placed 500-1000 years too early in time due to dating inaccuracies (Kaufman *et al.*, 2004), or alternatively that the first trees (poplar and birch) expanded in eastern Beringia from cryptic refugia (Brubaker *et al.*, 2005) or arrived from Siberia. The birch shrub tundra extended southward through most of the Yukon (Wang and Geurts, 1991; Cwynar and Spear, 1995) and probably into northern British Columbia, where alder was present as well (Miller and Anderson, 1974; Spear and Cwynar, 1997). There are few paleoecological sites in the latter region for this time. Evidence of boreal parkland

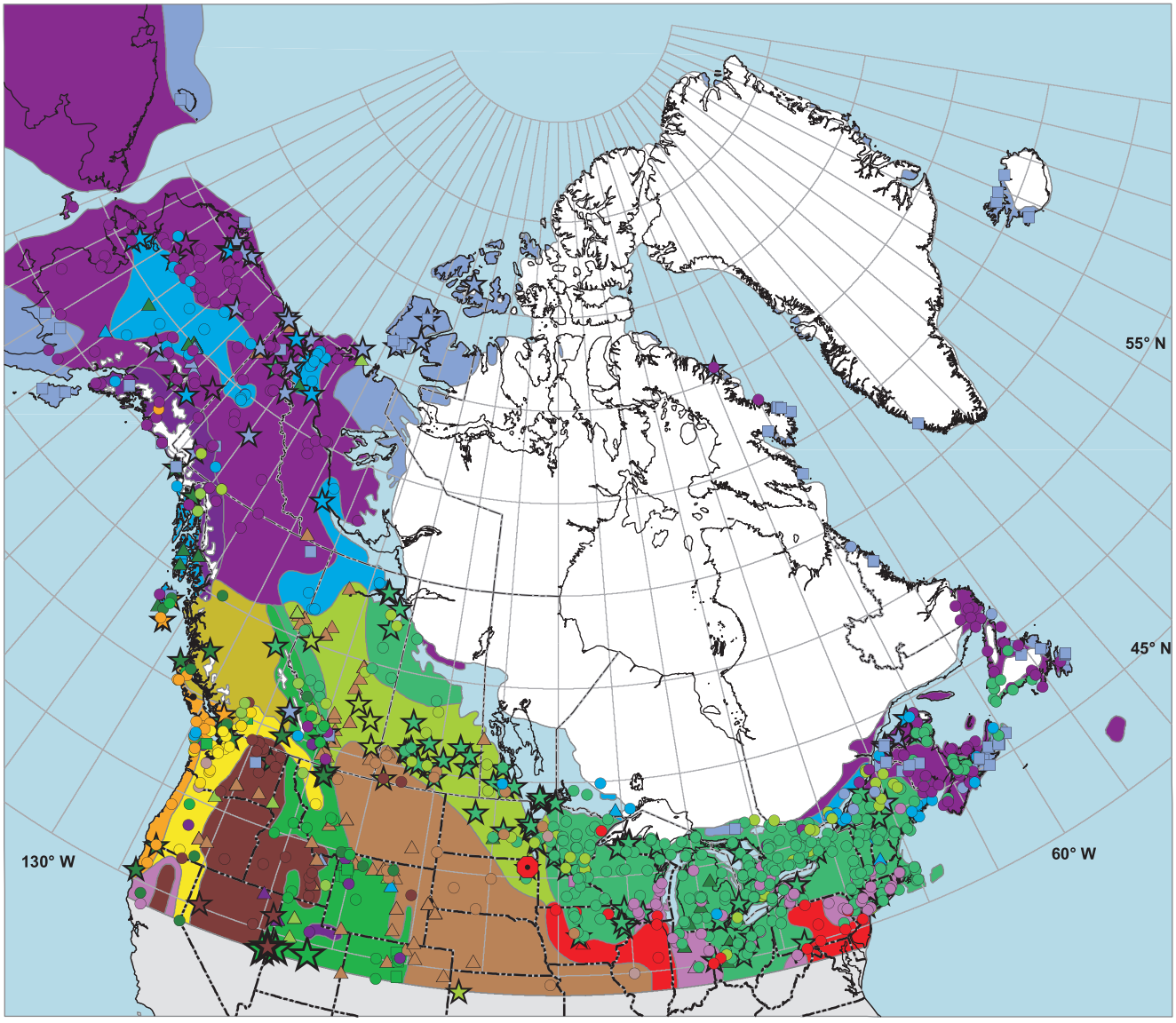


FIGURE 6. Biomes at 10 ka BP. *Les biomes en 10 ka BP.*

with poplar in the southwestern Yukon at 10 ka BP (Cwynar, 1988; Lacourse and Gajewski, 2000) may indicate inland extensions of the adjacent coastal forest tundra or that poplar forest tundra was more extensive in the Northwest than shown. Alternatively, these outlier sites may indicate anomalously old radiocarbon dates.

Shrub tundra with patches of boreal forest continued to characterize the Atlantic Provinces region of Canada (T. Anderson, 1980; Macpherson, 1981, 1996) as well as the periglacial zone from the Ottawa Valley to southeastern Labrador (Lamb, 1980; LaBelle and Richard, 1981; Engstrom and Hansen, 1985; T. Anderson, 1988; Harington *et al.*, 1993). Shrub birch was abundant throughout; juniper extended to Newfoundland and alder to Nova Scotia, New Brunswick and southeastern Québec.

In newly deglaciated areas of the Ottawa Valley and westward, the forest biomes shifted northward more quickly, apparently limited only by the rate of ice recession (Terasmae, 1980; T. Anderson, 1987; Bennett, 1987; Richard and Larouche, 1989; T. Anderson and Lewis, 1992). At 10 ka BP, the extent of the eastern boreal forest was being reduced by the northward expansion of the mixed forest accompanied by the migration north of 39 °N of deciduous forest in the mid-continent (King, 1981; Baker *et al.*, 1992) and in the Southeast (Watts, 1979). Nevertheless, in Ohio and vicinity, the spruce forest had expanded southward into what was earlier mixed forest, presumably as the result of Younger Dryas cooling (Shane, 1987, 1989). West of Lake Michigan, spruce- and jackpine-dominated forests were about equally common, with larch and fir important in the former and birch in the latter. The forest was similar in Michigan and Ohio, but jackpine-dominated forests were somewhat less common there. In Ontario, spruce was most abundant at about two-thirds of sites and jackpine at most others, with birch the next most common tree. Jackpine declined sharply in importance in New England. There spruce prevailed, and poplar and especially fir increased in importance.

The western part of the boreal forest was reduced due to northward expansion of the boreal parkland biome, which presumably reflects warming and (or) drying (Mott, 1973). Spruce appears to have been more prominent in the parkland than it is today, though poplar, birch and willow were also present (Lichti-Federovich, 1972; Mott and Christiansen, 1981; Vance, 1986). The western boreal forest at this time was an isolated disjunct that was separated from its eastern counterpart by parkland and by glacial Lake Agassiz. Here again white and black spruces were most abundant with white birch next in importance (Lichti-Federovich, 1970; Hutton *et al.*, 1994; McLeod and MacDonald, 1997).

Warming and drying also characterized the western regions at 10 ka BP. Warming in the American Rockies is indicated by a rise of treeline, replacing alpine tundra with subalpine forest of Engelmann spruce, subalpine fir, and whitebark pine on the Yellowstone Plateau of Wyoming and vicinity (Baker, 1983; Gennett and Baker, 1986; Whitlock, 1993; Whitlock and Bartlein, 1993) and in the mountains of northwestern Utah (Mehringer *et al.*, 1971). In the Colorado Front Range, treeline had been depressed during the Younger Dryas interval (Reasoner and Jodry, 2000) but was recovering by 10 ka BP (Short, 1985). Similarly treeline with lodgepole and whitebark pine, spruce, and fir rose to near present elevations in the central and southern Canadian Rockies at this time (Kearney and Luckman, 1983; Hills *et al.*, 1985; Reasoner and Hickman, 1989; Beaudoin and King, 1990; White and Osborn, 1992; Osborn *et al.*, 1995). Drying and warming in the American Southwest is echoed in the expansion of steppe at the expense of subalpine forest in the Great Basin region primarily of Idaho (Baker, 1976; Cotter *et al.*, 1986), by expansion of steppe into the Okanagan region of British Columbia (Hebda, 1982; Heinrichs *et al.*, 1999, 2001) and by the establishment of an interior forest biome characterized by Douglas fir replacing subalpine forest (Heusser, 1965; Hansen and Easterbrook, 1974; Barnosky, 1981; Cwynar, 1987; McLachlan and Brubaker, 1994). Drier and warmer conditions in southwestern British Columbia and Washington – 3-4 °C warmer than present by 10 ka BP according to chironomid assemblages (Walker and Pellatt, 2003) – allowed a forest of more "interior" composition (with more Douglas fir) to expand at the expense of coast forest. Central British Columbia at this time was covered by a conifer forest of mainly lodgepole pine with increasing Sitka spruce near the coast (Gottesfeld *et al.*, 1991; Hebda, 1995). This pioneer forest was presumably derived from the subalpine forest, which had occupied the Cordillera south of the ice sheet at 11 ka and earlier.

Drying and warming from the American Southwest to southwestern British Columbia and continued warming and moistening of Alaska is compatible with the northward shifting of the landfall of the jet stream, which perhaps awaited extensive deglaciation of the Cordilleran region. The great width of the tundra zone in the Canadian Maritimes is compatible with the concept of sustained northeasterly winds there caused by the persisting glacial anticyclone, which would have opposed wind dispersal of tree seeds into the region. Temperatures in this region were not to recover fully from Younger Dryas cooling until about 9.6 ka BP (Levesque *et al.*, 1997), implying that reduced heat transport in the Gulf Stream also continued to play a role in regional cooling if the thermohaline circulation mechanism for Younger Dryas cooling is correct (Broecker *et al.*, 1989). The lack of a tundra zone west of the Ottawa Valley suggests that direct periglacial cooling was less acute there than farther east and that temperate air masses strongly overlapped the ice margin. Intuitively, one expects the development of the large glacial lakes, starting about 11 ka BP, to have strongly affected the mid-continental climate. However, regional circulation model experiments indicate that the lakes essentially functioned as extensions of the ice sheet because of their low surface water temperatures and the expenditure of heat in the water on the melting of glacier ice and ice bergs (Hostetler *et al.*, 2000).

During the millennium ending at 10 ka BP – the interval generally acknowledged to have witnessed the terminal Pleistocene mammal extinction in North America, or at least its culmination – dryland grazers were still dominated by extinct forms of bison and by mammoths and horses (Table IV). There is nothing apparent in the record of dated faunal remains to suggest that extinction was caused by Younger Dryas cooling at 11 ka BP. Dated fossil specimens are as abundant in the 10.9-10 ka interval as in the preceding

interval and they are not clustered at the beginning of the interval. There was no apparent shrinkage of available grazing habitat – indeed grassland and steppe expanded between 11 and 10 ka BP – and it is not clear that any cooling event occurred on the grasslands themselves during the Younger Dryas. Similarly, mastodon remained by far the most commonly dated large mammal in the forested region during this interval, along with its familiar associates, the elk-moose and giant beaver (Table IV). Bison and mammoth continued to occupy forest openings and boreal parklands. Hence, unless all of the relatively late radiocarbon dates on the extinct taxa are erroneously young, the extinction event in the southern regions coincides with the end of the Younger Dryas interval; *i.e.*, with the onset of warming. The radiocarbon assays of concern (about 85) are nearly evenly split amongst conventional dates on bone collagen, AMS dates on bone collagen or extracts thereof, and conventional dates on associated wood or charcoal. There is no obvious reason for discarding all of them. It was also at about 10 ka BP that aboriginals in eastern and central North America changed the styling of their stone points from fluted projectile points to non-fluted forms that may have been used more commonly as knives, and shortly thereafter to side- and corner-notched projectile points (Ellis *et al.*, 1998). Possibly such changes reflect the changes of available faunal resources pursuant to extinction.

9 ka BP

By 9 ka BP, willow had spread through the herb tundra of much or all of the then-ice-free High Arctic (Fig. 7). Today it and allied woody shrubs (*e.g.*, *Cassiope tetragona*, *Dryas integrifolia*, *Vaccinium uliginosum*) extend to all but the northwestern fringe of the Canadian Arctic, where July mean temperature remains below 3 °C (Edlund and Alt, 1989). The oldest dated

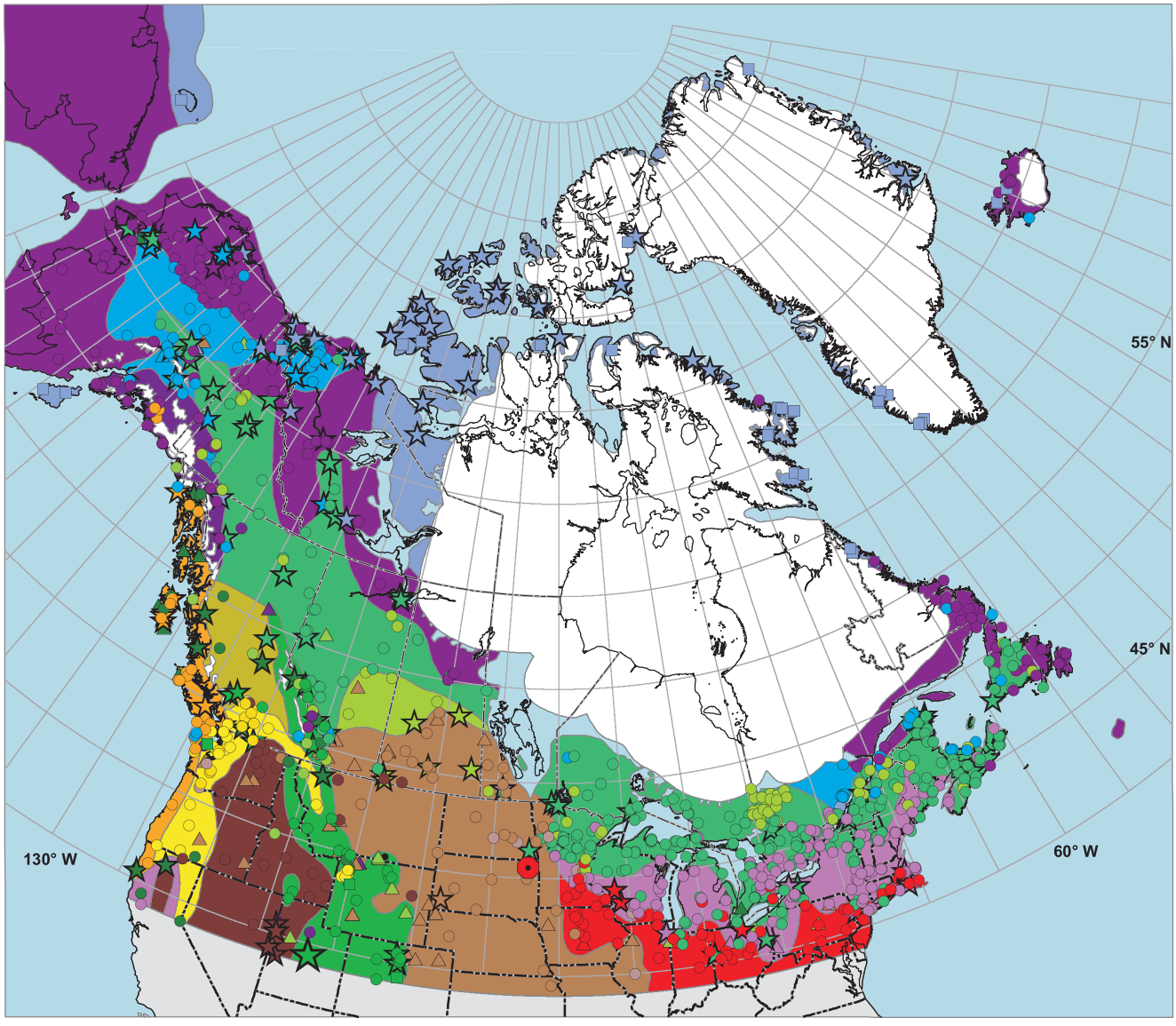


FIGURE 7. Biomes at 9 ka BP. *Les biomes en 9 ka BP.*

willow macrofossil (probably *Salix arctica*) in the region is 9.5 ka old from Somerset Island (Dyke, 1983). Bennike (1999) places the arrival of *Salix arctica* in Greenland at 8 ka BP, but *Salix glauca* and *Salix herbacea* evidently arrived there at 8.8 and 10.8 ka BP, respectively. There is also an indication that the forb component of the High Arctic tundra may have been more diverse at 9 ka BP than it is today. Seeds of the buttercup, *Ranunculus trichophyllus*, are found in peat dated 9.21 ka BP on Bathurst Island (Blake, 1974). It is apparently absent there today, though four other buttercup species do occur.

An orderly northward shifting of biomes occurred in the east between 10 and 9 ka BP. Birch shrub tundra extended far north along the Labrador coast, with alder reaching at least 53.2 °N and juniper at least 51.7 °N (Jordan, 1975; Short and Nichols, 1977). Shrub birch (*Betula nana*) also arrived in Iceland from European sources and juniper was established at some sites (Einarsson, 1963; Hallsdottir, 1990; Rundgren, 1995). Meanwhile boreal forest characterized by spruce with fir, white birch and jackpine, replaced shrub tundra through most of the Maritime Provinces, where small areas of mixed forest with oak were also established (Livingstone, 1968; Terasmae, 1973; Mott, 1975; Railton, 1975; Korpijaakko, 1977; Ogden, 1987; Jetté and Mott, 1989; Levesque *et al.*, 1993; Mayle *et al.*, 1993; Levesque and Cwynar, 1994; Mayle and Cwynar, 1995). A boreal forest of white spruce, black spruce, white birch, and balsam fir was established in the western half of Newfoundland as well, with alder arriving on the island about the same time (Macpherson and Anderson, 1985; Dyer, 1986). The boreal forest of Québec east of the Ottawa Valley was similar to that of the Maritimes, except that jackpine was unimportant and fir was abundant at about 20% of sites and important at many others. Elsewhere spruce was most abundant, with white birch, poplar, and alder the chief associates. The boreal forest of Ontario and the Great Lakes states was substantially different. Here jackpine was prominent at 64% of sites with birch and poplar most commonly associated. Most other sites were characterized mainly by spruce (32%), with birch, jackpine, and more rarely fir.

Mixed forest replaced the boreal forest in the southern Great Lakes region (Gilliam *et al.*, 1967; Manny *et al.*, 1978; Bailey and Ahern, 1981; Maher, 1982; Woods and Davis, 1989), in southern Ontario (Mott and Farley-Gill, 1978; Terasmae, 1980; T. Anderson, 1985; Yu *et al.*, 1996; Yu, 2000) and in much of New England (Whitehead and Chrisman, 1978; Whitehead, 1979; Ibe, 1982; Nelson, 1984; Whitehead *et al.*, 1989; Dunwiddie, 1990; Foster and Zebryk, 1993). White pine was common throughout this forest along with oak, elm, ash, birch, beech, and maple. Hemlock was important in the mixed forest in Ontario, Pennsylvania, and New York.

The deciduous forest extended northward, replacing boreal forest in Ohio (Shane and Anderson, 1993) and reaching its modern limit around Lake Michigan (Williams, 1974; Jackson *et al.*, 1986; Singer *et al.*, 1996). Oak was the most important tree throughout with elm, ash, hickory (*Carya* spp.), maple, birch, ironwood, and beech also widespread. Basswood occurred in Iowa and Illinois, chestnut (*Castanea* spp.) and gum (*Nyssa* spp.) in Pennsylvania, and hemlock in Pennsylvania and eastward.

The western boreal forest had expanded remarkably by 9 ka BP. It advanced northward into forest tundra along the Mackenzie Valley (MacDonald, 1987a), northwestward into tundra through northern British Columbia (MacDonald, 1987b; Pisaric *et al.*, 2003) and central Yukon (Cwynar, 1988; Keenan and Cwynar, 1992; Cwynar and Spear, 1995), reaching as far as central Alaska (Hu *et al.*, 1993). White and black spruce both migrated early and white birch was a significant component at many sites. Oddly, the forest tundra in the Alaska-Mackenzie region expanded only modestly between 10 and 9 ka BP. The boreal forest probably also extended southward into parkland reaching near to its modern southern limits in Alberta (Hickman and Klarer, 1981). Hazel (*Corylus* spp.) made a limited appearance in the Alberta parkland about this time, not appearing in pollen records again after 8 ka BP (Lichti-Federovich, 1970; note, however, that hazel pollen is difficult to identify and the shrub is common in the southern boreal forest now, A. Beaudoin, personal communication, 2005). However, the boreal parkland lost area to grassland in Saskatchewan (Kupsch, 1960; Ritchie and de Vries, 1964; Mott, 1973; Mott and Christiansen, 1981) and in Manitoba (Ritchie, 1967, 1969, 1976), where the grassland extended to Lake Agassiz, thus leaving the western boreal forest still disjunct from the eastern boreal forest.

The coast forest advanced northward through the Alaska Panhandle (Heusser, 1960; Hansen and Engstrom, 1996), possibly reaching the Prince William Sound area (Sirkin and Tuthill, 1987). Sitka spruce and alder with areas of lodgepole pine and poplar characterized this forest in Alaska and northwestern coastal British Columbia. However, western hemlock extended at least to 58.5 °N on the Alaska coast. In places alder formed stands (Peteet, 1986). In southwestern British Columbia, western hemlock, Douglas fir, and silver fir were most important, along with spruce, mountain hemlock, and alder in places. Western red cedar had reached Vancouver Island by this time, under conditions of maximum postglacial warmth between 10 and 9 ka BP (Walker and Pellatt, 2003). Red alder (*Alnus rubra*) seems to have been prominent in the coast forest of Washington, along with western hemlock, Sitka spruce, and Douglas fir (Heusser, 1973, 1978, 1983). Alpine treeline in southwestern British Columbia, in the Colorado Rockies, and probably in the Alberta Rockies was higher than present at 9 ka BP (Elias, 1985; Luckman and Kearney, 1986; Clague and Mathewes, 1989).

The pattern of vegetation changes between 10 and 9 ka BP reflects sustained warmth in the far northwest of North America, where it arguably had been warm enough to support trees since 11 ka BP, with increased effective moisture along the advancing southern margin of the western boreal forest in Alberta, but decreasing moisture farther east along the same boundary. Alternatively, forest expansion on the western plains between 10 and 9 ka BP may have resulted from megaherbivore extinction, whereas drier conditions farther east and closer to the ice sheet may reflect the drying influence of the glacial anticyclone.

Disappearance of the Late Pleistocene megaherbivores from the grassland and steppe biomes left bison as the dominant fossil mammal of the last 10 ka (Table VI). Although most

TABLE VI

The most common mammal fossils in various environments at 9.9-7 ka BP. Extinct or extirpated forms are marked with an asterisk

Mammal	9.9-9 ka	8.9-8 ka	7.9-7 ka
A. Steppe, Grassland and Savannah			
Bison *(Bison* spp., *B. bison bison, B.b. antiquus*, B.b. occidentalis*, B. priscus**)	51	48	48
Pronghorn (*Antilocapra americana*)	7	6	2
Elk *(Cervus* spp., *C. elaphus*)	4	3	4
Ground squirrel (*Spermophilus* spp., *S. mollis, S. richardsonii, S. townsendii*)	5	6	6
Beaver (*Castor canadensis*)	1	4	3
B. Conifer Forest, Parkland and Forest Tundra			
Bison *(Bison* spp., *B. bison antiquus*, B.b. bison*)	15	3	10
Elk (*Cervus elaphus*)	8	2	3
Caribou (*Rangifer tarandus*)	4	3	6
Moose (*Alces alces*)	13	5	9
Black bear (*Ursus americanus*)	8	2	4
Grizzly bear (*Ursus arctos*)	2		3
Beaver (*Castor canadensis*)	25	13	11
Muskrat (*Ondatra zibethicus*)	7	1	4
C. Tundra and Alpine Tundra			
Caribou (*Rangifer tarandus*)	2	2	8
Bighorn sheep *(Ovis* spp., *O. canadensis*)	5	4	3

abundant on the plains, bison extended through the boreal parkland and openings in the boreal forest, as wood bison (*Bison bison athabascae*) do today. Despite some loss of northern grassland and parkland on the Canadian prairies between 10 and 9 ka BP, large areas of grassland remained, making habitat loss seem an improbable cause of the extinction of the large grazers. In fact, the opposite has been argued – that the loss of herds of large grazers allowed the forest to encroach on grassland and parkland that had been maintained in part by grazing and tree destruction. Owen-Smith (1987) noted that the modern African elephant can, by its feeding and other activities, change a closed woodland into open grassy savannah within a decade and that the elimination of such animals could lead to fundamental biome changes. He views megaherbivores as keystone species, partly because their great size renders them immune to non-human predators, virtually ensuring that populations approach habitat carrying capacity. At that point their normal behaviour is an important control of biome dynamics. Hence, caution is again warranted in interpreting all vegetation changes in terms of climatic change, particularly around the time of the widespread large mammal extinctions.

Disappearance of the mastodon, elk-moose, woodland muskox, and giant beaver left the conifer forests to the moose, beaver, and muskrat (*Ondatra zibethicus*), with elk and woodland caribou (*Rangifer tarandus caribou*) exploiting open areas. The tundra caribou (*Rangifer tarandus tarandus*) extended northward through forest tundra and tundra. It is important to note here that these modern survivors amongst the large mammals are not seen as ecological replacements of the extinct taxa (Martin and Klein, 1984). That is, they do not occupy the same ecological niches. Hence, extinction cannot be seen as the result of competition from these modern forms.

Dreimanis (1968) noted that the extinction of the mastodon coincided with a change in composition of the boreal forest in the mid-continent from one characterized by spruce to one more characterized by jackpine. Table VII shows the percentages of spruce- and pine-dominated pollen assemblages in boreal forest and boreal parkland biomes as listed in the current database for 11, 10, and 9 ka BP. The increased abundance of pine, predominantly jackpine, was indeed a strong feature of the changing boreal forest composition in North America during that interval. However, pine never reached widespread dominance and at 10 ka, the approximate time of mastodon extinction, and spruce-dominated assemblages still outnumber pine-dominated assemblages in the available pollen records by more than two to one. If the mastodon became extinct because of loss of its main food source (spruce), something must have prevented it from moving to spruce-rich areas at 10 ka BP and earlier. Alternatively, the reduction of spruce-dominated forests in favour of pine during the interval of maximum regional mastodon populations (assuming that the number of dated specimens reflects population sizes) might be seen as the result of destruction of spruce seedlings and young trees by browsing mastodons.

8 ka BP

Dated macrofossils (GSC-2712) show that shrub willow had spread north at least to central Ellesmere Island by 8 ka BP (Fig. 8). Willow pollen increased at a lake on east-central Ellesmere Island at the same time (Hyvärinen, 1985).

TABLE VII

The percentage of spruce- and pine-dominated pollen assemblages in boreal forest and boreal parkland biomes at 11-9 ka BP

	11 ka	10 ka	9 ka
Spruce-dominated	90	66	51
Pine-dominated	5	25	37
Number of sites	258	287	284

Somewhat earlier, shrub willow increased in abundance in the herb tundra of eastern Baffin Island (Short *et al.*, 1985). Willows (*Salix arctica*, *S. herbacea* or *S. reticulata*) appear to have arrived in most of the eastern Canadian Arctic and Greenland between 9 and 8 ka BP, with *Salix glauca* also appearing in Greenland (Kelly and Funder, 1974; Fredskild, 1983, 1985). By 8 ka BP, shrub willows could have spread to Baffin Island from Labrador, from the north, or from Greenland.

By 8 ka BP, birch shrub tundra had advanced onto Banks Island in the western Canadian Arctic Archipelago (Gajewski *et al.*, 2000a) and east of Bathurst Inlet on the arctic mainland (Seppa *et al.*, 2003). Alder had spread through most of the shrub tundra of Alaska and the Yukon, reaching at least 70 °N and 165 °W on Seward Peninsula (Shackleton, 1979; Cwynar, 1982; P. Anderson, 1985), but had evidently not quite reached the Mackenzie Delta. Meanwhile alder had spread through the shrub tundra northwards along most of the Labrador coast to at least 58.6 °N (Clark *et al.*, 1989), but juniper does not appear to have extended much beyond its 9 ka limit in southern Labrador. Birch shrub tundra was well established in Iceland, where juniper also had become more widespread by 8 ka BP (Vasari, 1972; Hallsdottir, 1996; Wastl *et al.*, 2001). However, the warmest part of Greenland, which

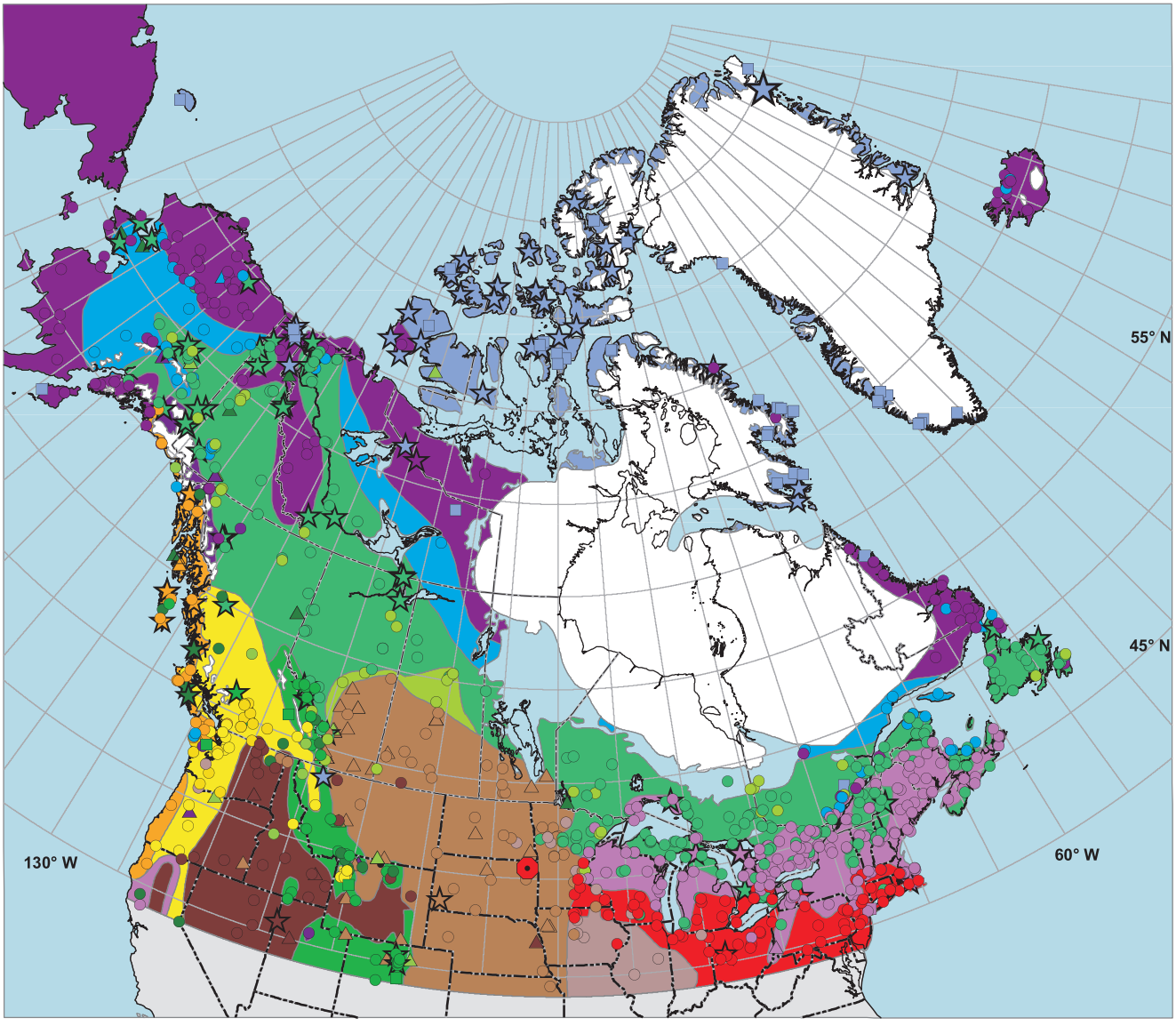


FIGURE 8. Biomes at 8 ka BP. *Les biomes en 8 ka BP.*

today supports birch, alder, and juniper shrub tundra with occasional tree birch, retained its cover of herb tundra dominated by grass, sedge, heather, and arctic willows (Fredskild, 1972, 1973; Kelly and Funder, 1974; Fredskild, 1983, 1985). Nevertheless, summer lake water temperatures and mean annual air temperatures, based on chironomid assemblages and ^{18}O concentrations in chironomid head capsules, respectively, were at postglacial maximum levels by 8 ka BP (2° and 4°C warmer than present, respectively; Wooller *et al.*, 2004).

The western and eastern boreal forests remained separated by glacial Lake Agassiz-Ojibway. The western boreal forest expanded only modestly, mainly northward along the Mackenzie Valley, where treeline advanced nearly to the coast and beyond present treeline (Ritchie and Hare, 1971; Hyvärinen and Ritchie, 1975; Ritchie, 1977; Ritchie *et al.*, 1983; Ritchie, 1984a, 1984b, 1985, 1987). The beaver evidently expanded its range in step with treeline, as shown by a lodge dated to 7.8 ka BP in the present tundra on Kendal Island off the Mackenzie Delta (Mackay, 1971). Forest expansion in Alaska was slow in comparison, although forest tundra expanded toward the southwest and farther onto Seward Peninsula (Hopkins *et al.*, 1981; Ager and Brubaker, 1985; Brubaker *et al.*, 2001). The northern part of the western boreal forest was mainly white spruce, black spruce, and white birch; alder spread within the forest to at least 68.5 °N (Ritchie, 1987). White and black spruce also characterized the southern part of this forest with white birch; pine, probably jackpine, became more important in northern Alberta, whereas aspen, poplar, and alder were more common in northern British Columbia.

The southern boreal tree limit moved northward on the plains as the grassland attained its maximum extent since 11 ka BP both northward (Hickman and Klarer, 1981; Hickman *et al.*, 1984; MacDonald, 1989; Hickman and Schweger, 1996) and northeastward (McAndrews, 1966; Janssen, 1968; Waddington, 1969; Dean *et al.*, 1984; Jacobson and Grimm, 1986; Almquist-Jacobson *et al.*, 1992; Hu *et al.*, 1997). Grassland expansion was accompanied by opening of the boreal forest margin in northwestern Ontario to form parkland, at least locally, accompanied by extension of the range of plains bison (*Bison bison bison*) (McAndrews, 1982). Farther south in the grassland of southeastern Nebraska, increased aridity between 9 and 8 ka BP led to near elimination of gallery woodlands along streams (Baker *et al.*, 2000).

The limit of the eastern boreal forest expanded very slowly toward Labrador between 9 and 8 ka BP (Richard, 1973, 1975; Mott, 1976; King, 1986; Garralla and Gajewski, 1992; Richard *et al.*, 1992; Lavoie and Filion, 2001). Treeline advance was slow here probably because the narrow strip of periglacial terrain between the ice sheet and the ocean remained chilled due to continued proximity of the ice front or due to the persistence of anticyclonic northeasterly winds off the Labrador Sea. However, the boreal forest completed its expansion in Newfoundland between 9 and 8 ka BP (Macpherson, 1996). As a whole, the eastern boreal forest was somewhat reduced in area, because of the northward expansion of mixed forest (Saarnisto, 1974; McAndrews, 1981; Heide, 1984; Szeicz and MacDonald, 1991) during an interval when the northern forest margin was held in check by large glacial lakes that occupied the topographic slope toward Hudson Bay.

The eastern boreal forest was more diverse than its western counterpart at 8 ka BP. In Ontario and the Ottawa Valley margin of Québec, jackpine was the most abundant tree in the majority (60%) of sites, with birch the most common associate and most abundant at about 20% of sites; forests characterized mainly by spruce were relatively rare (14% of sites), and fir was an uncommon associate. In Québec east of the Ottawa Valley and in the Appalachian Mountains of New Hampshire and Maine, fir was the most important tree, particularly in the more oceanic regions, such as the Gaspé Peninsula of Québec, with spruce being next most common. Spruce and pine were the main components in New Brunswick and Prince Edward Island, with birch and fir the most significant associates. In Newfoundland, where balsam fir dominates much of the forest today, spruce was more important at most sites at 8 ka BP. Fir and white birch were the most significant associates, both widespread, along with alder in more open areas.

The mixed forest had expanded through much of northern New England and the Maritimes by 8 ka BP and it even extended beyond its modern limit in places, such as north of Lake Superior. White pine remained the most common tree throughout this biome, as at 9 ka BP. West of Lake Huron, the most important associates were oak, elm, and birch. In Ontario and New York, oak and hemlock seem to have been the most common trees, with hemlock reaching greatest abundance – and in places being the most important tree – in New York. In Maine and the Maritimes, oak, fir, hemlock, and birch were the chief associates.

The deciduous forest expanded close to its modern northern limit, and somewhat farther in places, such as in Massachusetts (Ogden, 1963). As at 9 ka BP, the oaks were the most common trees throughout this biome. Hickory and beech were widespread, whereas elm, ash, and ironwood seem to have declined in importance in the east and birch in the west. Hemlock was important in Ontario, Pennsylvania and New England, and maple was most prominent within this biome in Ontario. Meanwhile the southern limit of the deciduous forest moved northeastward leaving oak savannah in its wake in Indiana, Illinois, and Iowa. This change indicates a warming and drying of the eastern Great Plains (Brush, 1967; King, 1981).

The same climatic trend is indicated by northward expansion of interior forest and interior parkland in central British Columbia and by the establishment of this forest in presently wet areas of eastern Vancouver Island and the Fraser Lowland (Hebda, 1983). Douglas fir, lodgepole pine, and in places Ponderosa pine were the key trees here, with alder, western hemlock, Sitka spruce, and fir as associates. The adjacent coast forest had almost reached its limit along the south coast of Alaska, having advanced to at least 142 °W (Heusser, 1965).

Continued warming and drying in the American Cordillera led to further expansion of steppe from the Great Basin into high ground previously occupied by subalpine forest in Wyoming (Albanese and Frison, 1995), thus fragmenting that forest biome. Meanwhile alpine timberline remained above present elevations in Colorado, Alberta, and southern British Columbia (see above and Elias, 1983; Luckman 1988; Clague and Mathewes, 1989).

Although mammal distributions continued to shift in response to overall biome shifts and changes in plant assemblages,

virtually the full extent of the continent had been occupied by 8 ka BP. For example, the dwarf Peary caribou (*Rangifer tarandus pearyi*) had expanded to the north coast of Ellesmere Island by 8.4 ka BP (Stewart and England, 1986) and had reached Greenland by 8 ka BP (Meldgaard, 1986). Thus herb tundra in the highest arctic had achieved a carrying capacity comparable to that of the present shortly after local deglaciation.

LATE DEGLACIATION (7.5-5 KA BP)

This interval starts with the fragmentation of the Laurentide Ice Sheet, caused by deglaciation of Hudson Bay, and ends with the final disappearance of glacier ice in Québec-Labrador. Although the glacial anticyclone probably dissipated as a quasi-permanent feature with the opening of Hudson Bay, the remnant ice masses during this interval were still large enough to affect regional climate in their vicinities, but evidently not far afield.

7 ka BP

Although herb tundra probably prevailed on eastern Baffin Island (Miller *et al.*, 1999), dwarf birch seems to have gained a foothold in places as far north as Clyde Inlet by 7 ka BP (Fig. 9; Short *et al.*, 1985), and as far north as Cumberland Peninsula by 8 ka BP (Fréchette *et al.*, 2003). It is unclear whether the earliest birch on Baffin Island was *Betula glandulosa* from Labrador or *Betula nana* from Greenland. The latter has a restricted distribution on southeastern Baffin Island today (Porsild, 1957; Andrews *et al.*, 1980) and it is the less thermophilous of the two.

Shrub tundra also may have made its initial appearance in southwest Greenland by 7 ka BP (Kelly and Funder, 1974). Here green alder (*Alnus crispa*) and juniper seem to have arrived ahead of dwarf birch, the opposite of the sequence seen in Canada and Alaska. Alternatively, the strong rise in

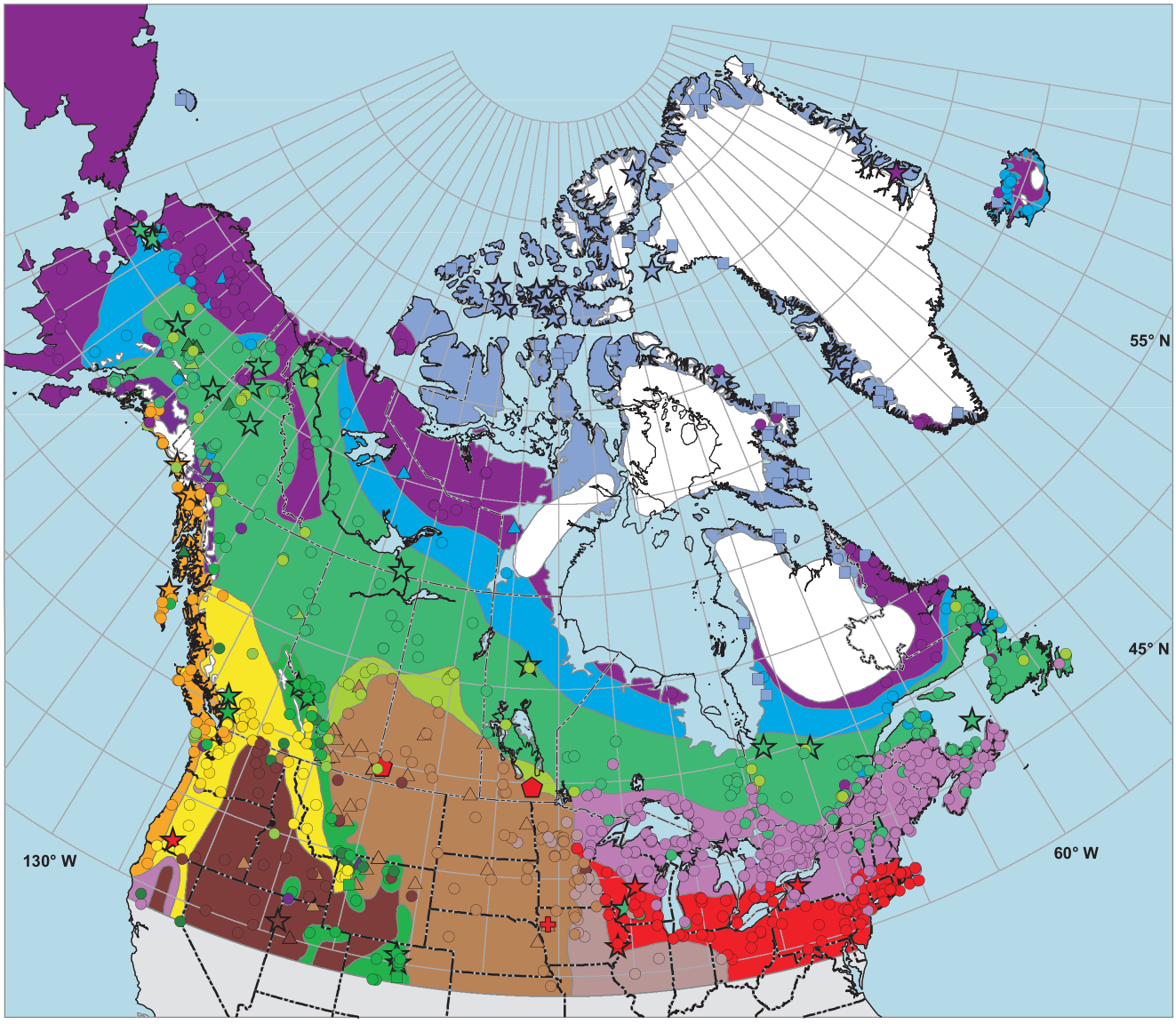


FIGURE 9. Biomes at 7 ka BP. *Les biomes en 7 ka BP.*

alder pollen at sites in Greenland at 7.6 ka BP may reflect enhanced long-distance transport resulting from the spread of alder northward along the Labrador coast after 8 ka BP as discussed above, and an increase of easterly winds over the Labrador Sea pursuant to diminution of the glacial anticyclone over eastern North America. Evidently this is the general interpretation accepted by Bennike (1999), who places the arrival of alder in Greenland at 4.4 ka BP. Nevertheless, Bennike accepts the arrival of juniper (*Juniperus communis*) in Greenland at 7.8 ka BP, in agreement with Kelly and Funder (1974). Dwarf birch (*Betula nana*) had reached Scoresby Sund in East Greenland from Iceland by 7 ka BP as shown by dated macrofossils (Böcher and Bennike, 1996). Plants in Greenland arrived most commonly from Iceland and – at least in the case of alder – from Labrador (Bennike, 1999). The shrub tundra of Labrador at 7 ka BP was characterized by alder and birch, as before, and juniper seems not to have spread northward along the coast between 8 and 7 ka BP. Alder was widespread in the shrub tundra of Alaska and eastward to the Mackenzie Delta by 7 ka BP, but failed to spread much to the east of there during postglacial time. In Iceland, a partial cover of forest tundra with tree birch (*Betula pubescens*) – the only forest tree to reach the island in the Holocene – had been established (Hallsdottir, 1996).

The boreal forest at 7 ka BP was an unbroken biome extending from Alaska to Newfoundland and Labrador. Latitudinal treeline fell somewhat short of its present position across most of Alaska, although forest tundra extended beyond the present limit of trees on Seward Peninsula, where beavers had been present since at least 9.4 ka (McCulloch *et al.*, 1965). Similarly, the boreal forest still extended beyond its present limit in the Mackenzie Delta region. The limit of boreal forest farther east fell somewhat short of its present position (Nichols, 1972a, 1975; Ritchie, 1979). However, forest tundra extended nearly to modern treeline, which probably indicates inadequate in-fill (densification) time since deglaciation for full forest development. The most rapid spread of boreal forest between 8 and 7 ka BP was into southern Labrador from its previous limit in the vicinity of Lac Saint-Jean (Lamb, 1980; Engstrom and Hansen, 1985).

As before, the boreal forest at 7 ka can be considered in three sections from a compositional point of view. West of Ontario, spruce was most abundant at almost all sites, with both black and white spruce well represented. Pine was most common at a few sites in Alberta and aspen in British Columbia. White birch was the major associate throughout and alder was important in British Columbia and regions to the north and west. In Ontario and the Ottawa Valley region of Québec, jackpine was most abundant at about two-thirds of sites in the boreal forest and spruce at others. White birch was the most common associate of jackpine, and jackpine the most common associate of spruce; fir remained unimportant. In Québec, southeastern Labrador, and Newfoundland, spruce was most common at about half of reported sites in the boreal forest, balsam fir at about a third, and white birch at the rest. Furthermore, fir was a major associate at about half the sites characterized by spruce or birch. Fir seems to have attained its greatest prevalence in southeastern Québec, where it remains important or dominant today, and it was an aggressive colonizer in southeastern Labrador. Yellow birch, probably the most thermophilous element in the Newfoundland forest today, where it has a restricted distribution, arrived on the Avalon Peninsula about 7 ka BP (Terasmae, 1963), as did black ash (*Fraxinus nigra*), which survives in the area today as a shrub (Dyer, 1986).

Meanwhile, the mixed forest boundary was well north of its present location in the region from Lake of the Woods to the Ottawa Valley (Vincent, 1973; Bjorck, 1985; Liu, 1990, McIntyre *et al.*, 1991) and this biome had penetrated farther into New England and Québec (Richard, 1970, 1973, 1975, 1977, 1980). The deciduous forest boundary was north of its present location in the southern Great Lakes region (McMurray *et al.*, 1978; Heide, 1984), the grassland and parkland boundaries remained somewhat north of their present locations on the Canadian prairies, and treeline remained above present elevations in the Colorado and Alberta Rockies and in the British Columbia Coast Range. Conditions were so dry on the prairies by 7.5 ka BP that there was insufficient inflow of water to the southern basin of Lake Winnipeg to fill the basin to overflow despite the fact that isostatic tilting was tending to raise water levels at the south end of the lake (Lewis *et al.*, 2001). The moisture balance at Winnipeg may have been similar to that at Medicine Hat today. Conditions also may have been sufficiently dry in the Great Lakes region at about the same time to draw water levels in the Huron Basin below overflow levels (Blasco, 2001). But evidently they were not so dry as to desiccate the regional mixed forest. Continued expansion of the mid-continent savannah and grassland biomes into areas formerly occupied by mixed and deciduous forest (Wright *et al.*, 1963; McAndrews, 1966; Cushing, 1967; Durkee, 1971; Grimm, 1983; Brugam *et al.*, 1988; Baker *et al.* 1992; Baker and Drake, 1994) indicates further warming and drying there, as does replacement of subalpine forest by drier interior forest (Mehringer *et al.*, 1977) and by steppe (Albanese and Frison, 1995) in the mountains of Montana. In contrast, a re-expansion of coast forest in the Puget Sound region indicates greater effective moisture in the Pacific Northwest (Heusser, 1985). Summer temperatures there were about 2 °C above present values but had declined from the postglacial maximum (Walker and Pellatt, 2003).

The mixed and deciduous forest biomes continued to be characterized by much the same taxa as previously. White pine continued to characterize most regions of the mixed forest, except in New England, where it was somewhat exceeded by hemlock, and in Québec, where maple and yellow birch were more important. From Minnesota to Michigan, oak was the most important associate followed by birch, elm, and ironwood. In Ontario, hemlock was most common at about 25% of sites and birch, oak, beech, elm, and maple were strongly represented. Hemlock had also become most common in places in Maine and the Maritimes, and oak, birch, and fir remained widespread there. Oak was most common everywhere in the deciduous forest, except for occasional stands of elm, maple, beech or hemlock in Ontario, beech in Michigan, and basswood in Iowa. Elm, ironwood, hickory, and basswood were the prominent associates in the western part of the forest (Michigan westward); elm, beech, maple, hickory, and ash in the central part (Ohio, Ontario); and hemlock, beech, hickory, and chestnut in the east.

These middle Holocene conditions in the central and eastern part of the continent can be understood as a consequence of the disappearance of the glacial anticyclone with deglaciation of Hudson Bay at 7.6 ka BP, combined with a summer radiation receipt that was 6% greater than at present. Although a brief cold event followed deglaciation of Hudson Bay due to oceanographic changes in the North Atlantic caused by proglacial lake drainage (Barber *et al.*, 1999), elimination of the blocking anticyclone permitted strengthening and northward shifting of prevailing westerly winds over the prairies and Ontario while in southeastern Québec-Labrador the westerlies replaced prevailing northeasterly winds, both warming the region during summer and assisting in plant dispersal.

The ascendance of jackpine in the central part of the eastern boreal forest, starting about 10 ka BP and peaking 9-7 ka BP, possibly indicates maximum dryness in that region. Jackpine and white birch, its most common associate at the time, are both early successional trees that are intolerant of shade. Jackpine relies on fire for the release of seeds from its cones, which otherwise remain sealed by resin with a melting point above the range of air temperatures. It is therefore improbable that these two species would have replaced a closed spruce forest in the absence of frequent, major fires. However, lake sediment charcoal records offer only inconsistent support for this hypothesis (Fuller, 1997). The mechanism of replacement of spruce forests by jackpine-birch forests is thus still under discussion. Wright (1968) and Wright *et al.* (2004) argued that the climate simply became too warm for spruce to regenerate and jackpine took over as the spruce forest opened with the death and windthrow of spruce trees. On the other hand, Critchfield (1985) argued cogently for replacement because of fire disturbance. The case for the warming hypothesis would be strengthened had a more thermophilous pine replaced the spruce. Jackpine has a rather restricted distribution in the mixed forest today, whereas white spruce does quite well there.

6 ka BP

By this time the biomes were in essentially modern positions, except in areas of late deglaciation, of which the most significant were northern Québec-Labrador and Baffin Island (Fig. 10). Shrub tundra expanded in Labrador and Québec, where both birch and alder spread quickly after deglaciation (Short and Nichols, 1977; Lamb, 1985a, 1985b; King, 1985, 1986). Shrub tundra also expanded in southwest Greenland, where juniper and birch (*Betula nana* and *B. glandulosa*), and possibly green alder (see above) were present (Fredskild, 1973, 1983, 1985). *Betula nana*, however, is not a strict indicator of Low Arctic conditions; it extends well into the High Arctic tundra of northeast Greenland today, although it has not reached High Arctic Canada during the Holocene (Porsild, 1957; Andrews *et al.*, 1980). Shrub tundra expansion in Greenland indicates either continued warming or continued plant migration under already favourable conditions, because the ice sheet was as small as it is presently by 6 ka BP. The chironomid-inferred temperatures in southwest Greenland were declining by this time but were still about 1 °C warmer than present (Wooller *et al.*, 2004). Shrub tundra failed to expand at this time on Baffin Island from the few putative sites of earlier establishment (Short *et al.*, 1985; Fréchette *et al.*, 2003).

The main change in boreal forest distribution between 7 and 6 ka BP was a large northward advance in Québec-Labrador (Mott, 1976; Richard, 1979; Richard *et al.*, 1982; King, 1985, 1986), a consequence of deglaciation, preceded by an expansion of forest tundra. Larch was a pioneering tree in the forest tundra of central and western Québec (Gajewski *et al.*, 1993, 1996), but evidently not in Labrador. The forest limit also advanced nearly to the Hudson Bay coast in Ontario and Manitoba (McAndrews *et al.*, 1982; Dredge and Mott, 2003), advanced slightly in the Great Bear Lake area (Nichols, 1972b) and advanced significantly westward in central Alaska (Edwards and Brubaker, 1986; Brubaker *et al.*, 1983; Hu *et al.*, 1996). Similarly forest tundra expanded into the Thelon River basin (Craig, 1959) and into the mountains west of the Mackenzie River (Szeicz *et al.*, 1995), although treeline was retracting slightly in the vicinity of the Mackenzie Delta. The largest compositional change in the boreal forest involved a reduction of the preponderance of jackpine in Ontario to being most common at less than one-third of sites from two-thirds a millennium earlier, with black and white spruce predominating elsewhere. In Québec and Labrador, spruce and fir remained the most common trees at nearly equal numbers of sites. Spruce and fir also predominated in Newfoundland, where larch appears to have become more important than previously. White pine, red pine (*Pinus resinosa*), and ash – all thermophilous and evidently never abundant in Newfoundland – appeared at this time and attained their greatest abundance during the next 2000 years (Macpherson, 1995). White and black spruce remained exceedingly common in the western boreal forest, though jackpine may have increased somewhat in Saskatchewan and Manitoba (Nichols, 1967; Mott, 1973; Ritchie and Haden, 1975; Ritchie, 1976, 1980; Ritchie and Yarranton, 1978; Wilson, 1981; Dredge and Mott, 2003).

Warmer-than-present conditions in the mid-continent are indicated by the continued more northerly distribution of mixed forest from Lake of the Woods to Ottawa Valley, where white pine pushed well north of its present limit (T. Anderson and Terasmae, 1970), by the somewhat more northerly placement of the boundaries of grassland and boreal parkland on the prairies (Vance *et al.*, 1995), by higher than present treelines in the Rocky Mountains of Alberta and southwestern British Columbia (above and Luckman *et al.*, 1993), and by the greater extent of steppe in northeastern Washington and Idaho (Mack *et al.*, 1978, 1979; Baker, 1983). Vance described similar biome departures from present at 6 ka BP for Canadian territory (in Gajewski *et al.*, 2000b).

The faunal record for the middle and late Holocene (Table VIII) is dominated by collections from archaeological sites. Because of the increasing visibility of younger sites and the better preservation of younger bones, there is a general increase in the abundance and diversity of taxa recorded through time that does not necessarily carry any climatic implication. Furthermore, remains at these sites preferentially reflect those animals that were important food, clothing and other resources. Detailed analyses of assemblages of environmentally specialized small mammals reveal some changes

during the middle and late Holocene as well as some still-disharmonious mammal assemblages (Graham *et al.*, 1987). However, by 6 ka BP the distribution of larger mammals by biome groups was unsurprising. Modern bison, elk, mule deer (*Odocoileus hemionus*), and pronghorn were prevalent on the grasslands and ranged into the boreal parklands; white-tailed deer (*Odocoileus virginianus*), elk and black bear (*Ursus americanus*) are the most abundant remains from the mixed and deciduous forests; moose, caribou, black bear, and snowshoe hare (*Lepus americanus*) are most abundant in the conifer forests; caribou, moose, and snowshoe hare, in the forest tundra; and caribou, muskox, arctic fox (*Alopex lagopus*), arctic hare (*Lepus arcticus*), and polar bear, in the tundra. Beaver and muskrat were exploited in all biomes south of the continental treeline (Canadian Archaeological Radiocarbon Database, 2005).

5 ka BP

The major changes between 6 and 5 ka BP were the northward expansion of biomes in the eastern Arctic and Subarctic (Fig. 11). Alder-birch shrub tundra and forest tundra expanded in Québec-Labrador (McAndrews and Samson, 1977; Richard, 1979; Stravers, 1981; Gajewski *et al.*, 1993, 1996), and larch extended to a point somewhat beyond its present range (needles dated 4.96 ka BP; Richard, 1981). Birch (*Betula glandulosa*) shrub tundra advanced broadly onto southern Baffin Island (Short *et al.*, 1985; Jacobs *et al.*, 1990; Escamilla, 1994; Jacobs *et al.*, 1997) and juniper and birch (*Betula glandulosa* and *B. nana*) shrubs continued to expand their range in southwest Greenland (Fredskild, 1983; Eisner *et al.*, 1995).

Elsewhere changes were subtler. The limit of forest tundra and boreal forest advanced in southern Nunavut and southeastern Northwest Territories (*i.e.*, the mainland west of

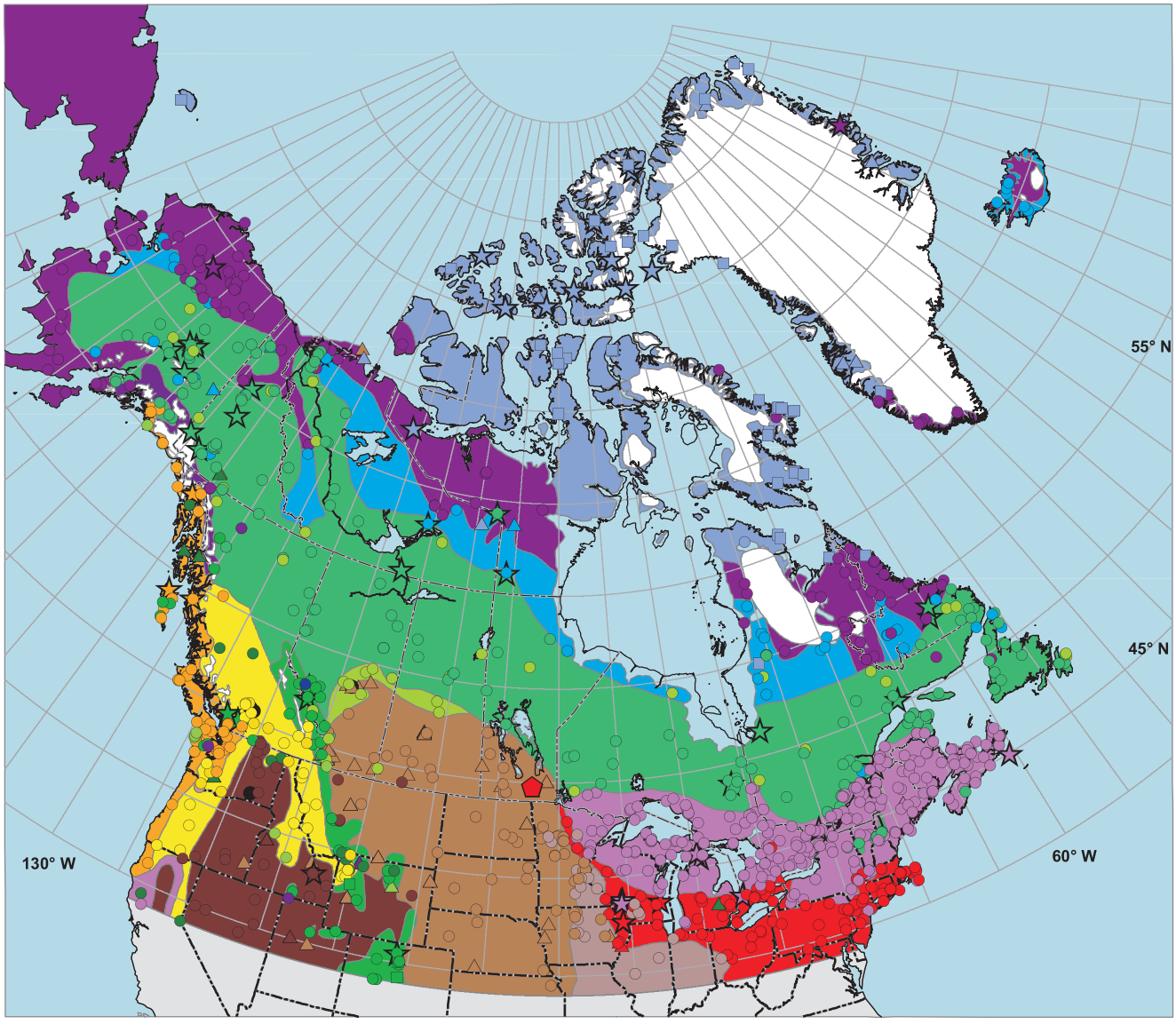


FIGURE 10. Biomes at 6 ka BP. *Les biomes en 6 ka BP.*

TABLE VIII

The most common mammal fossils in various environments at 6.9-0 ka BP

Mammal	6.9-5 ka	4.9-3 ka	<3 ka
A. Steppe, Grassland and Savannah			
Bison *(Bison* spp., *B. bison bison*)	113	150	806
Pronghorn (*Antilocapra americana*)	36	28	151
Deer *(Odocoileus* spp., *O. hemionus*)	27	22	81
Elk (*Cervus elaphus*)	20	14	37
Wolf (*Canis lupus*)	10	3	28
Coyote (*Canis latrans*)	10	3	21
Ground squirrel (*Spermophilus* spp., *S. richardsonii, S. tridecemlineatus*)	26	22	81
Pocket gopher *(Geomys* spp., *G. bursarius*)	3	1	19
Gopher (*Thomomys* spp., *T. talpoides*)	17	8	35
Cottontail *(Sylvilagus* spp.)	23	7	51
Beaver (*Castor canadensis*)	4	5	61
Muskrat (*Ondatra zibethicus*)	5	1	20
B. Deciduous and Mixed Forest			
Deer *(Odocoileus* spp., *O. virginianus*)	6	32	195
Elk (*Cervus elaphus, C.e. canadensis*)	1	5	38
Bear *(Ursus* spp., *U. americanus*)	2	21	81
Beaver (*Castor canadensis*)	5	31	120
Muskrat (*Ondatra zibethicus*)	5	13	83
Raccoon (*Procyon lotor*)		10	73
C. Conifer Forest and Parkland			
Bison *(Bison* spp., *B.b. athabascae*)	9	57	106
Elk (*Cervus elaphus*)	5	50	84
Moose (*Alces alces*)	28	41	113
Caribou (*Rangifer tarandus*)	3	2	54
Deer *(Odocoileus* spp., *O. hemionus*)	23	58	129
Bear *(Ursus* spp., *U. americanus*)	11	39	104
Hare *(Lepus* spp., *L. americanus*)	6	37	98
Beaver (*Castor canadensis*)	26	71	209
Muskrat (*Ondatra zibethicus*)	1	16	74
Porcupine (*Erethizon dorsatum*)	5	29	53
D. Forest Tundra			
Caribou (*Rangifer tarandus*)	9	14	81
Moose (Alces alces)			20
Elk (*Cervus elaphus*)	2	1	3
Hare *(Lepus* spp., *L. americanus*)	2		16
Beaver (*Castor canadensis*)	2		16
E. Tundra			
Caribou (*Rangifer tarandus*)	13	79	389
Tundra muskox (*Ovibos moschatus*)	2	44	173
Sheep (*Ovis canadensis, O. dalli*)	5	4	16
Arctic fox (*Alopex lagopus*)		19	107
Arctic hare (*Lepus arcticus*)		23	60
Polar bear (*Ursus maritimus*)		6	73

Hudson Bay; Kay, 1979; Edwards *et al.*, 1996) but apparently changed little between there and the Mackenzie Delta, where treeline remained north of its present location. The boreal forest essentially completed its slow expansion through central and southwestern Alaska between 6 and 5 ka BP (P. Anderson, 1985, 1988), that expansion lagging long after the Holocene thermal maximum (Kaufman *et al.*, 2004). Boreal (aspen) parkland, grassland, mixed forest, and deciduous forest biomes maintained more northerly distributions than present. The deciduous forest boundary retreated and forest was replaced by grassland in Iowa and Wisconsin (Baker *et al.*, 1990; Chumbley *et al.*, 1990) but deciduous forest possibly advanced at the expense of savannah in Ohio and Indiana. These changes indicate a complexly changing effective moisture distribution on the eastern Great Plains, where air masses from the Pacific (dry east of the Cordillera) and from the Gulf of Mexico (moist) are in frequent contact. Alpine treeline was above its present elevation in those areas where it was high a millennium earlier and in the southwestern Yukon (Denton and Karlén, 1977).

POSTGLACIAL (AFTER 5 KA BP)

Significant changes of glacier ice cover after 5 ka BP were limited to Baffin Island (Dyke, 2004).

4 ka BP

The most thermophilous postglacial vegetation development was delayed until 4-3 ka BP in areas of very late deglaciation and in certain areas where plants evidently migrated rather slowly. By 4 ka BP, birch shrub tundra had reached or exceeded its modern limit on Baffin Island (Fig. 12). Neither juniper nor alder extended so far north during the

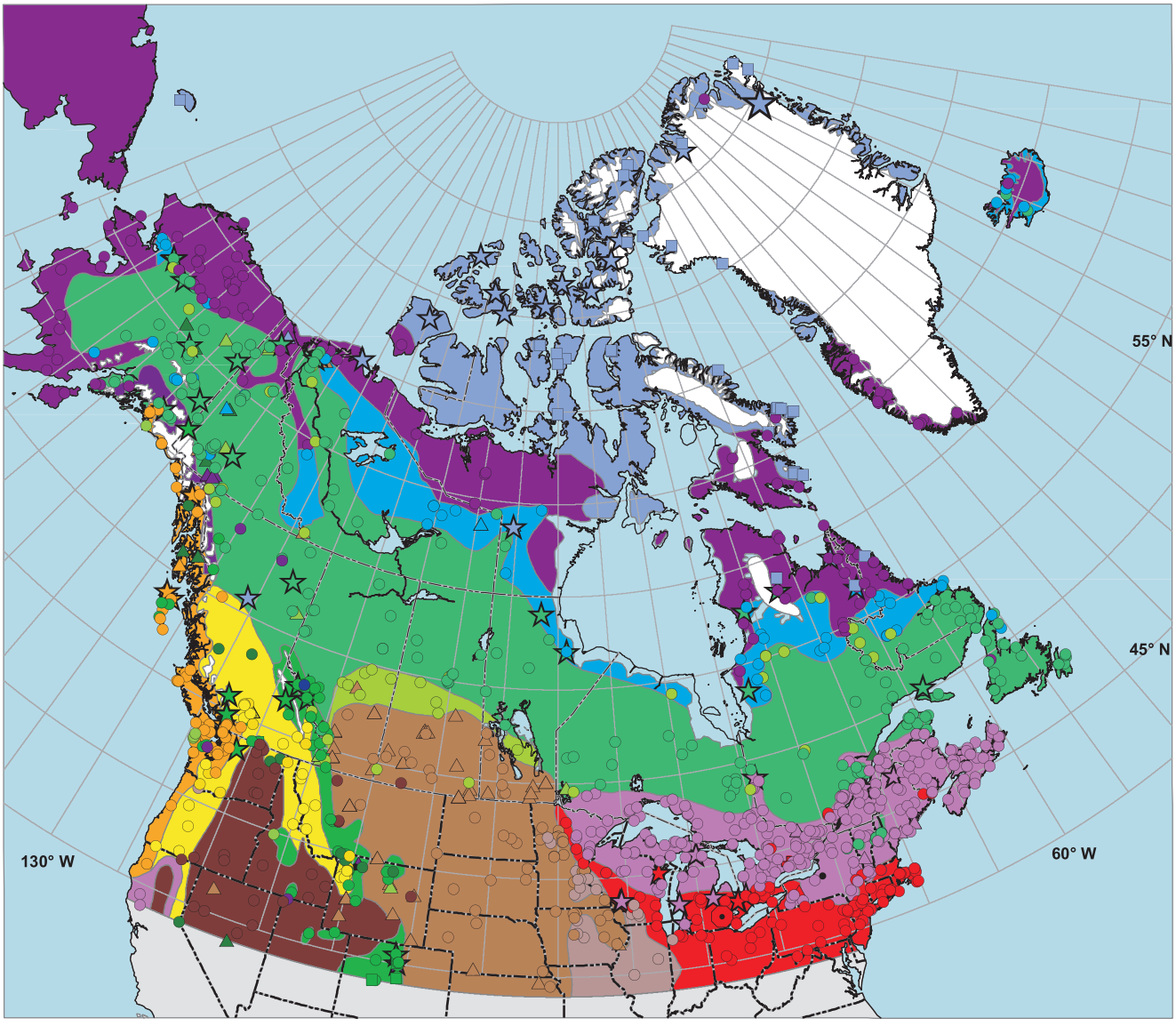


FIGURE 11. Biomes at 5 ka BP. *Les biomes en 5 ka BP.*

Holocene. Shrub tundra was nearly at its limit in West Greenland (Fredskild, 1985), where green alder had arrived from Labrador and tree birch (*Betula pubescens*) from Iceland (Bennike, 1999). The latter exists in a small part of southernmost Greenland, which is therefore classified in some schemes as Subarctic, rather than Low Arctic (Funder, 1989). Forest tundra was approaching its modern limit in northeastern Québec-Labrador (Short and Nichols, 1977; Williams *et al.*, 1995). Forest tundra and boreal forest remained north of their present positions in the Dubawnt Lake-Ennadai Lake region of Nunavut, based on macrofossils dating from 3.54-4.0 ka BP (Bryson *et al.*, 1965; Nichols, 1972b). Treeline was slightly beyond its present position in the Mackenzie Delta and somewhat higher than present in the mountains to the southwest, where spruce macrofossils are dated at 4.4 ka BP (Szeicz and MacDonald, 2001) and in the southwest Yukon, where a spruce log 76 m above treeline was dated to 3.6 ka BP (Denton and Karlén, 1977). Boreal forest continued to expand along the south coast of Alaska, reaching Kodiak Island, as did the northern limit of the coast forest in that state (Heusser, 1985). Forest tundra continued its expansion into shrub tundra in southwest Alaska between 5 and 4 ka BP (Hu *et al.*, 1995).

In other areas, biomes were retracting from more northerly positions at 4 ka BP. The northern grassland boundary retracted to near its modern position and a positive moisture balance inside the adjacent boreal forest allowed the paludification front to advance southward (Zoltai and Vitt, 1990). However, the boundary between deciduous forest and grassland or savannah remained east and north of its present position in most places. The northern boundary of mixed forest continued its slow withdrawal in Ontario although remaining north of its present position (Julig *et al.*, 1990). In the mid-continent, in contrast, deciduous forest was at its most northerly

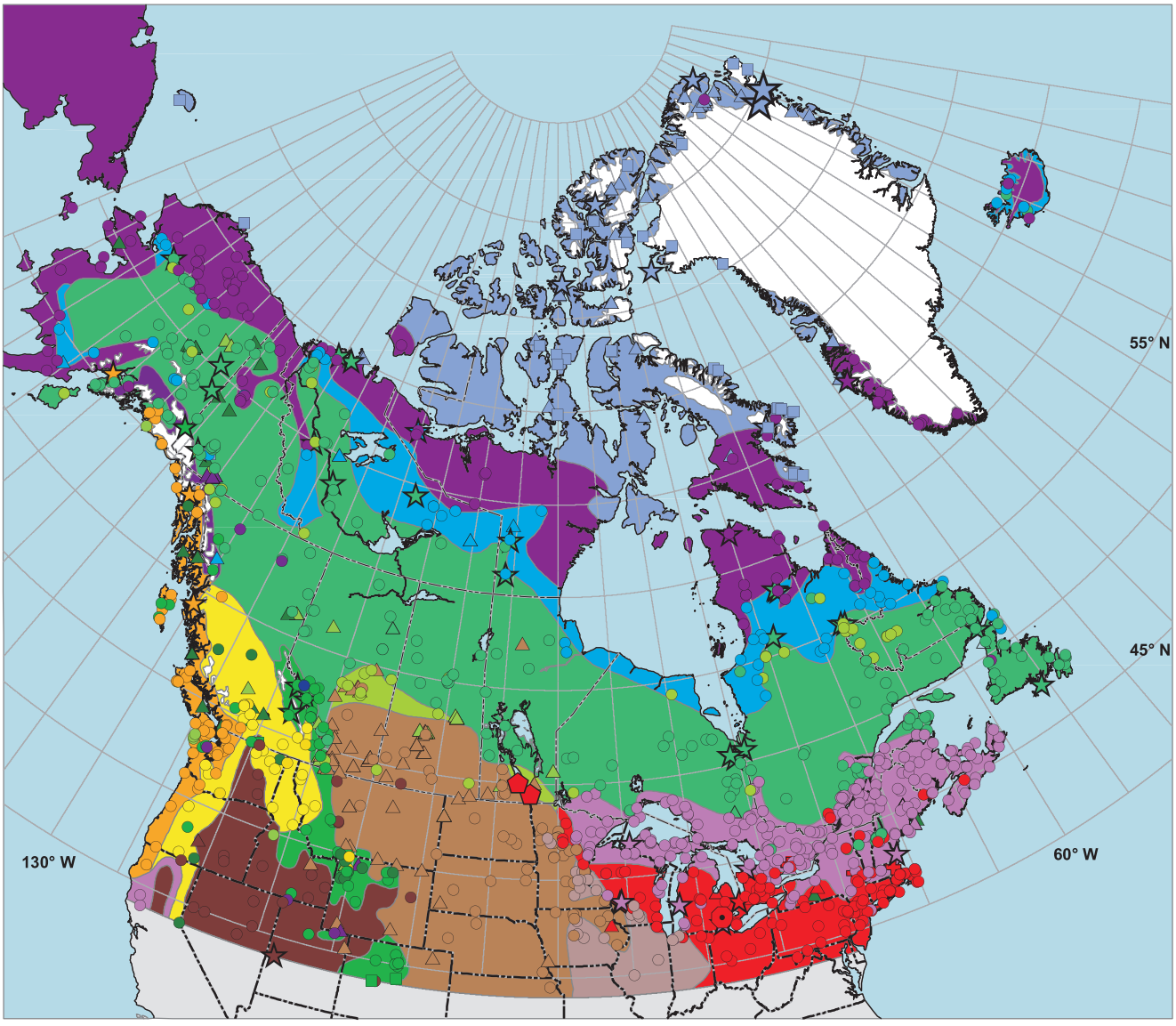


FIGURE 12. Biomes at 4 ka BP. *Les biomes en 4 ka BP.*

postglacial position (Sreenivasa, 1973; Karrow *et al.*, 1975; Webb *et al.*, 1983; Turner *et al.*, 1983; Heide, 1984). However, this was mainly a consequence of the loss of hemlock in the mixed forest, which rendered the resulting forest in its southern part more purely deciduous. Eastern hemlock, a major species in the mixed forest, was greatly reduced in abundance over most of its range at 4.8-4.5 ka BP. It has been argued that the reduction was the result of a pathogen (Davis, 1981) – most likely an infestation by an insect, the hemlock looper (Bhiry and Filion, 1996). However, there is also macrofossil and lake-level evidence that the hemlock decline was driven by severe drought, which might also have stimulated insect outbreaks and left the trees more susceptible to death by defoliation (Haas and McAndrews, 1999; Shuman *et al.*, 2004). Eastern hemlock regained its modern extent mainly in the last 2000-3000 years, but never regained its former prominence, presumably because of competition from trees that occupied its former stand areas. Its partial recovery may have been assisted by moister conditions attending Neoglacial cooling in the mixed forest region (it requires a minimum annual precipitation of 710 mm; Brugam and Johnson, 1997). The interior forest of Douglas fir, lodgepole pine, and Ponderosa pine in northeastern Washington and Idaho expanded at the expense of steppe as a result of cooling and moistening (Mack *et al.*, 1978, 1979), and western red cedar became more prominent in the coast forest of British Columbia for the same reason (Hebda and Mathewes, 1984). Thus, climate trends at 4 ka BP seem to have been spatially complex, with temperature-limited biomes advancing northward toward modern limits in the eastern Arctic and Subarctic and in southern Alaska but retracting southward towards modern limits in central Canada.

3-1 ka BP

The main biome distribution changes during the late Holocene (Figs. 13-15) involved the southward retraction of

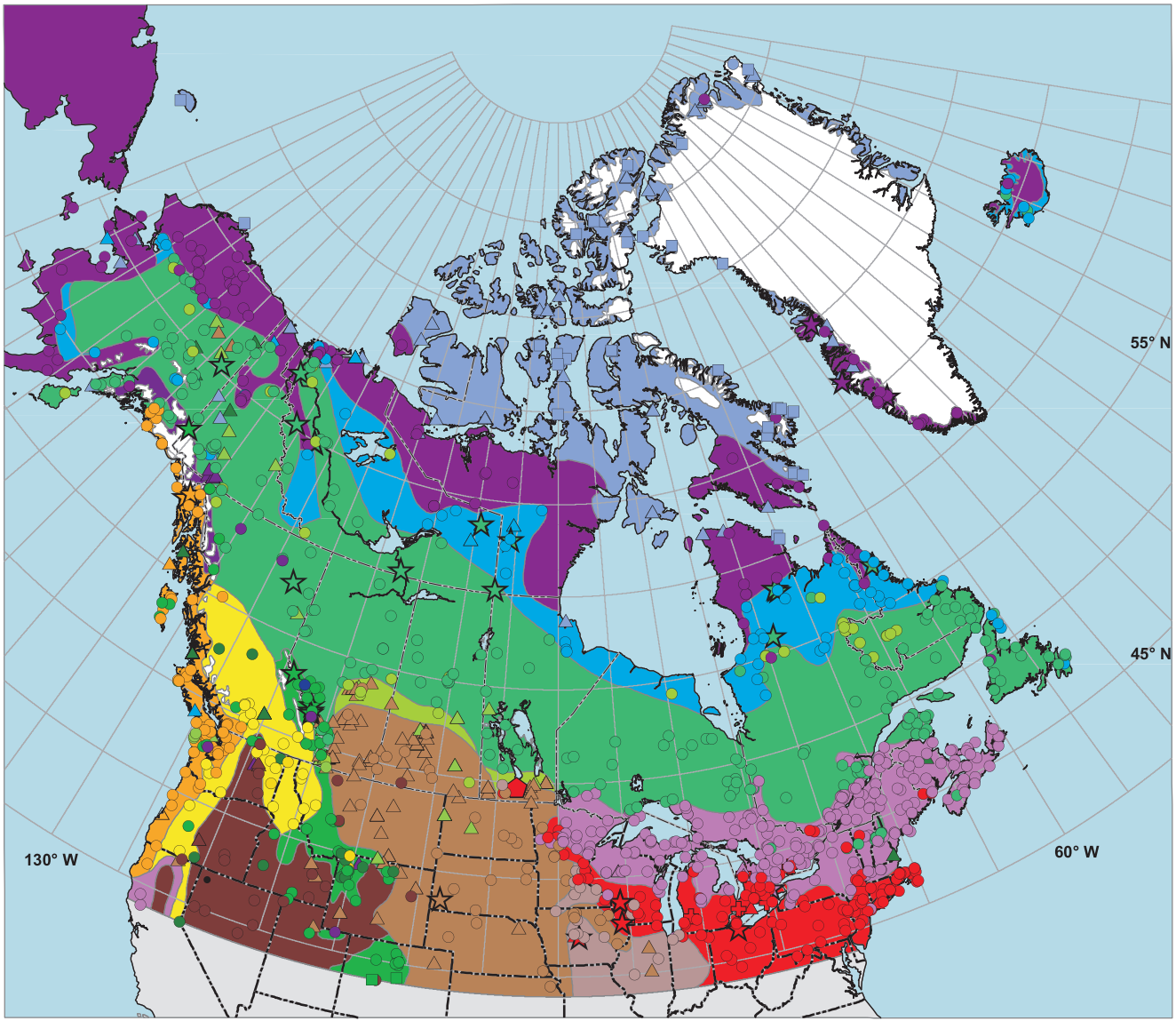


FIGURE 13. Biomes at 3 ka BP. *Les biomes en 3 ka BP.*

the northern limits of biomes and of species ranges and the lowering of alpine treelines. This occurred during a period recognized globally as the Neoglacial, a period generally cooler than the earlier parts of the Holocene (Denton and Karlén, 1973). Although the Neoglacial included intervals that were both warmer and colder than the early part of the 20th century – for example, the so-called Medieval Warm Period and the Little Ice Age – these events are proving to have been spatially complex in terms of temperature patterns and were not always globally or even hemispherically synchronous (Bradley and Jones, 1993). Biome distribution changes in response to these 0.3-1 °C temperature fluctuations were subtle. By 1 ka BP (Fig. 15), all biome limits were close to their present positions on present evidence.

Few changes are documented from the High Arctic, but biotic response to late Holocene cooling probably exceeded what can be presently shown in this poorly studied region. An interesting, but uniquely documented, event is the disappearance of *Salix arctica* from the Pearyland region of northeast Greenland at 3.9 ka BP (Funder and Abrahamsen, 1988), indicating that the July mean temperature declined below 3 °C. Possibly, it was about this time that woody shrubs disappeared from the 'barren wedge' of the Canadian polar margin. Similarly, the moss, *Scorpidium scorpoides*, which had extended north to Bathurst Island in the central High Arctic until 2.76 ka BP, was thought to have died out there sometime thereafter (Brassard and Steere, 1968; Blake, 1974). It has since been reported living on adjacent Prince of Wales Island (Gajewski and Frappier, 2001), but this occurrence may be a relict of range retraction. On Somerset and Prince of Wales islands, a general reduction of ground cover by plants in the last 3 ka is registered by reduced pollen production particularly by willow (*Salix arctica*), heather, sedge, and sorrel (Gajewski, 1995; Gajewski and Frappier, 2001). In the herb tundra of Banks Island, grasses expanded at the expense of sedges during the last 3 ka, which is also taken as a sign of cooling (Gajewski *et al.*, 2000a).

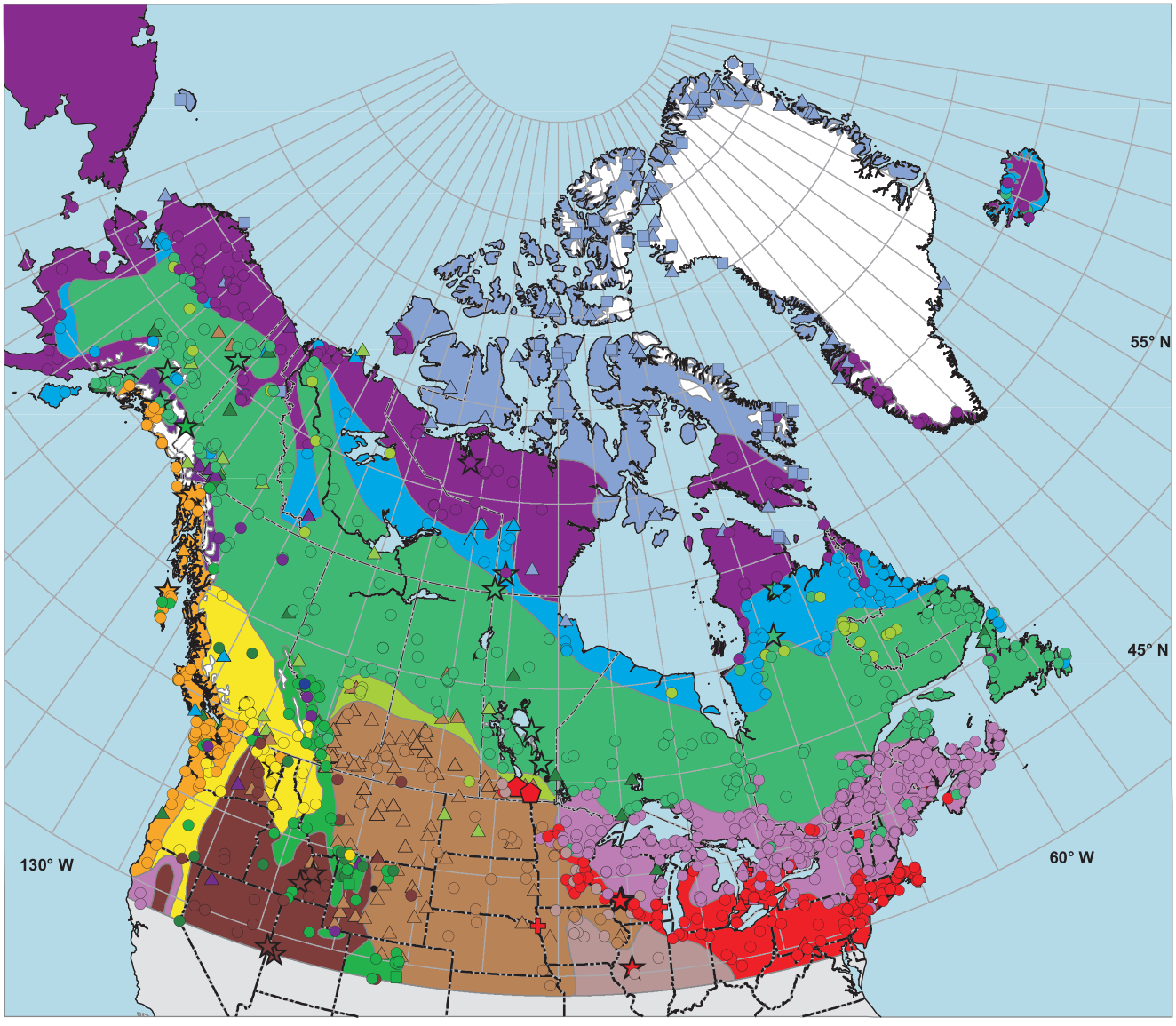


FIGURE 14. Biomes at 2 ka BP. *Les biomes en 2 ka BP.*

Shrub tundra retracted in the eastern Canadian Arctic (Short *et al.*, 1985) and in West Greenland (Fredskild, 1985; Funder, 1989) during the same period.

At 3 ka BP, treelines were still somewhat higher than present in the central Canadian Rockies, in the Mackenzie Mountains, and in the St. Elias Mountains of the Yukon, and in Colorado (references cited above; Carrara *et al.*, 1991). Treelines fell as alpine glaciers advanced shortly thereafter. Similarly, the range of larch was reduced at the forest tundra limit in northwestern Québec (Gagnon and Payette, 1981). The boreal forest limit retreated slightly in southern Nunavut (Kay, 1979), in the central Northwest Territories (Nichols, 1972a; Moser and MacDonald, 1990), and in the Mackenzie Delta region (Ritchie and Hare, 1971; Spear, 1983). It evidently maintained its position in Alaska, except on Kodiak Island, where boreal forest with tree birch reverted to forest tundra with scattered Sitka spruce by 2 ka BP (Heusser, 1985). The northern limits of the mixed and deciduous forests retreated slightly in the mid continent. This recession was primarily due to retraction of the northern range of white pine in the Lake Superior region (Liu, 1990; Flakne, 2003) and the increasing abundance of that tree in Lower Michigan (Bailey and Ahern, 1981; Holloway and Bryant, 1985). It was also due to the resurgence of hemlock in the northern fringe of the deciduous forest in southern Ontario and northwestern New York (Sreenivasa, 1973; Spear and Miller, 1976). The grassland boundary in Minnesota and Wisconsin retreated westward between 4 and 3 ka BP, but it appears to have been fairly stable thereafter (McAndrews, 1966; Grimm, 1983; Dean *et al.*, 1984; Holloway and Bryant, 1985; Jacobson and Grimm, 1986). Hence, the late Holocene presents widespread evidence of general cooling across the continent, even at this coarse biome level of analysis.

There were also important compositional changes within biomes that more finely reflect cooling and moistening during

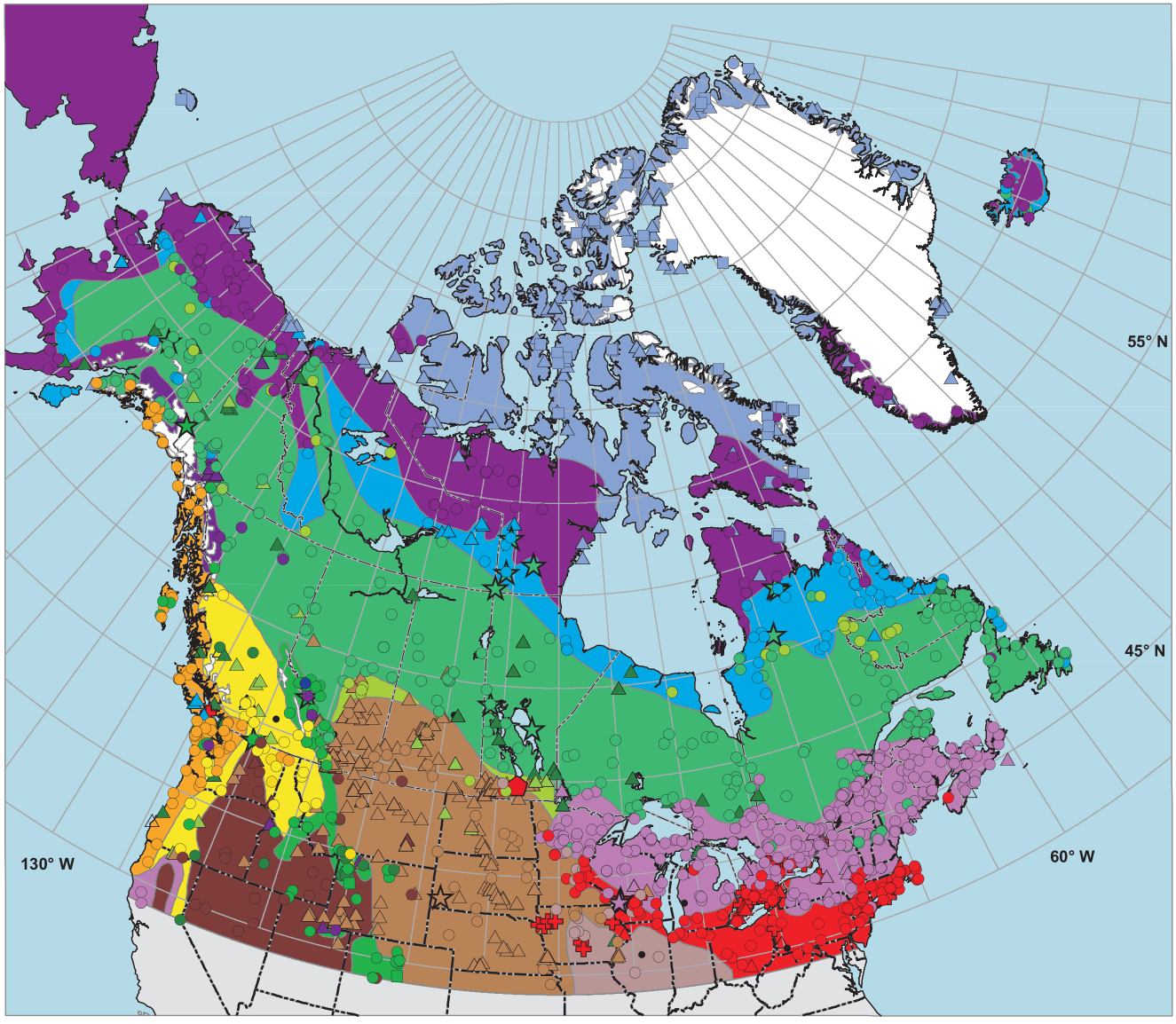


FIGURE 15. Biomes at 1 ka BP. *Les biomes en 1 ka BP.*

the last 3000 years. For example, the northern boreal forest and forest tundra in Québec became less dense and more shrubby (Richard *et al.*, 1982), fir increased in importance in the boreal forest in Newfoundland (Macpherson, 1995), and spruce showed a marked increase as a significant component throughout much of the eastern mixed forest zone, particularly in the last 1000 years (see review by Schauffler and Jacobson, 2002). Thus, not only did the mixed forest retreat somewhat, but also it took on a more boreal character (Table IX). Similarly, western hemlock, a moisture demanding species, expanded into the subalpine zone of southeastern British Columbia starting at about 3.5 ka BP and mountain hemlock appeared about 2.1 ka BP, suggesting an opening of the forest there due to cooling (Rosenberg *et al.*, 2003). A high-resolution pollen analysis of a site in the northern edge of the deciduous forest in Ontario shows a strong decline of beech and concurrent rise of oak and white pine pollen in response to cooling during the Little Ice Age starting 1450 A.D. (Campbell and McAndrews, 1993). That study showed that the vegetation response remained in disequilibrium with climate for more than 650 years as individual species were advantaged or disadvantaged by canopy opening that resulted from the death of beech. Unfortunately there are few studies with such fine temporal resolution.

TABLE IX

The percentage of sites showing spruce-dominated and co-dominated pollen assemblages in the mixed forest biome at 3-1 ka BP

Mixed forest association	3 ka	2 ka	1 ka
Spruce dominated	4	8	20
Spruce co-dominated (with white pine, hemlock or birch)	9	14	14
Number of sites classified as mixed forest	196	199	208

SUMMARY OF TREELINE POSITIONS

Figure 16 draws together all macrofossil dates that indicate when altitudinal and latitudinal treelines, or tree species limits near treeline, were higher than or north of their present positions. In Alaska (Hopkins *et al.*, 1981) and at one alpine site in Alberta at least (Luckman and Kearney, 1986), treelines exceeded present positions just prior to the Younger Dryas. There is no direct macrofossil evidence of higher or more northern treelines during the Younger Dryas cold interval (11-10 ka BP), which is perhaps not surprising. During the millennium after the Younger Dryas interval, treelines exceeded present positions both latitudinally and in elevation in the far Northwest (Northwest Territories, Yukon, and Alaska; Hopkins *et al.*, 1981; Nelson and Carter, 1987), in southwestern British Columbia (van Ryswyk, 1971; Clague and Mathewes, 1989), and in Colorado (Elias, 1985; Carrara *et al.*, 1991). Abundant sites indicate higher than present treelines in the Cordillera and more northern treelines in the Northwest from 9 to about 5 ka BP. As before, these sites are distributed from Alaska to Colorado (Detterman, 1970; Esdale *et al.*, 2001; citations earlier in paragraph). The relative paucity of sites dating between 5 and 3.5 ka BP possibly indicates that treeline was near its present elevation at that time. However, the sites with wood of this age have the same distribution as before 5 ka, except that additional sites from late-deglaciated Keewatin and Québec appear in this interval. The concentration of sites dating 3.6-2.8 ka BP may indicate a new advance of treeline or simply the maintenance of higher and more northern treelines until 2.8 ka BP. These sites are distributed from Québec and Keewatin (mainland Nunavut) to Alaska and Colorado. After 2.8 ka BP, the evidence suggests retreat of the larch limit in northwestern Quebec (Gagnon and Payette, 1981) and

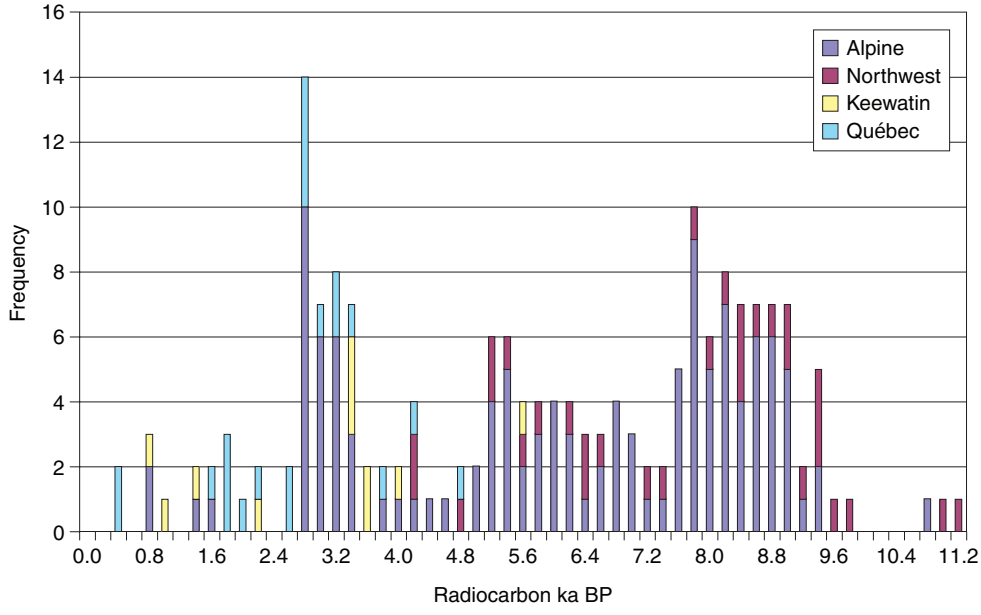


FIGURE 16 Radiocarbon dates on tree remains that grew above (Alpine) or north of (all others) present treeline.

Dates au radiocarbone de restes d'arbres qui ont poussé au-dessus (étage alpin) ou au nord de la limite de pousse des arbres actuelle.

perhaps brief intervals of treeline advance in Keewatin, in the St. Elias Range and in south-central British Columbia.

Hence, at its simplest, this distribution of radiocarbon dates indicates a warmer than present middle and early Holocene and a cold Neoglacial with brief warm intervals. Magnitudes of minimum treeline displacement indicated by these sites tend to be in the range of 50-300 m for alpine treeline, which implies temperature changes of as much as 3 °C, a value generally in accordance with estimates of Holocene thermal maximum temperature increases (Kaufman *et al.*, 2004). Mid-summer latitudinal temperature gradients in Canada are about 1 °C per 100 km (National Atlas of Canada). Therefore, as a rule of thumb, we might expect a sustained future summer warming of 3 °C to force biome boundaries northward by about 300 km. Temperature gradients are less than that in areas of greater continentality, most conspicuously in the Interior Plains region of Saskatchewan, Alberta, and the Northwest Territories. Larger shifts might be expected there.

BIOME MIGRATION RATES

We will consider postglacial biome migration rates along several lines of section drawn in the direction of overall biome expansion during deglaciation. Rates are given in both radiocarbon and calendar time scales using the conversions in Stuiver *et al.* (1998).

Section A-B of Figure 17 illustrates migration of biome boundaries through time along a line from the American Midwest to the south shore of Hudson Bay, a line essentially normal to the receding ice margin. The northern limit of the boreal forest advanced 1 490 km between 18 and 6 ka BP (21.4 and 6.8 calendar ka BP), at an average rate of 124 m per ^{14}C yr (102 m per calendar year). During two intervals – 14 to 12 ka and 8 to 7.6 ka BP – the northern limit of boreal forest advanced more slowly than the ice front retreated and forest tundra or tundra appeared briefly before the forest arrived. Possibly these were times when the rate of ice recession exceeded the ability of forest limits to advance due to edaphic, biotic, or climatic limitations. The average rate of advance of the forest limit by 450 km between 14 and 12 ka BP (16.8 and 14 calendar ka BP) was 225 m per ^{14}C yr (161 m per calendar year). Between 10 and 8 ka BP (11.35-11.55 to 8.85-9.0 calendar ka BP; 11.45-8.92 calendar ka BP using the mid points of the radiocarbon plateaus), the boreal forest limit advanced 510 km at an average rate of 255 m per ^{14}C yr (202 m per calendar year). These latter two are *tabula rasa* rates of advance where there was no competition from other trees and when the climatic conditions may have well exceeded threshold values required to support the species of concern, primarily white and black spruce. However, the advance of more ice-distal biomes occurred by replacement of their northerly predecessors. The mixed forest biome appears on the line of section at 10 ka BP. By 7 ka BP (7.8 calendar ka BP), it had advanced 680 km at an average rate of 227 m per ^{14}C yr (186 m per calendar year). Similar slopes of the lines in Section A-B indicate that other biome boundaries migrated by replacement of pre-existing biomes at similar rates of 100-200 m per year. After 7 ka BP, the northern limit of the mixed forest retreated 150 km at an average rate of 19 m per calendar year.

Section C-D extends from northeastern USA to central Québec-Labrador. Between 14 and 5.8 ka BP (16.8 and 6.6 calendar ka BP), the ice retreated 1520 km at an average rate of 185 m per ^{14}C yr (149 m per calendar year). During most of that interval trees advanced along this line rapidly enough that there was only brief and patchy establishment of herb or shrub tundra, notably during the Younger Dryas interval of retarded ice recession. Hence, between 13 and 5 ka BP (15.65 and 5.75 calendar ka BP), the northern boundary of the boreal forest advanced 1 500 km at a nearly constant rate of 188 m per ^{14}C yr (152 m per calendar year). Between 11.5 and 8 ka BP (13.45 and 8.92 calendar ka BP), the mixed forest advanced 825 km at an average rate of 236 m per ^{14}C yr (182 m per calendar year) by replacement of boreal forest.

Section E-D extends from southwestern Nova Scotia to central Québec-Labrador. As stated earlier temperatures had risen sufficiently by 12 ka BP to support forest, but shrub tundra still prevailed. Forest tundra briefly extended into the region just before 11 ka BP but was eliminated by Younger Dryas cooling, when summer temperatures were depressed below those required to support spruce growth. Between 10 and 9.5 ka BP (11.45 and 10.7 calendar ka BP), boreal forest spread across the entire region at a rate of about 1 000 m per ^{14}C yr (667 m per calendar year). However, the pattern of biomes at 10 ka BP indicates that this exceptionally high rate may represent the aggregate expansion of several coalescing forest patches. Mixed forest spread into the same region between 8.5 and 7 ka BP (9.5 and 7.8 calendar ka BP) at a rate of 320 m per ^{14}C yr (282 m per calendar year). Advance of the boreal forest limit between 7 and 5 ka BP (7.8 and 5.75 calendar ka BP) at 220 m per ^{14}C yr (215 m per calendar year) was only slightly slower than the rate of ice recession.

Section G-F extends from Montana to the Mackenzie Delta. After 13 ka BP the line of section is strongly oblique to the direction of ice recession but is more-or-less normal to biome boundaries. Because the central part was the last to be deglaciated, vegetation invaded from both the south and the north. The oddity of exceptionally early forest tundra in the far north may well be the result of anomalously old radiocarbon dates, as discussed above; its appearance might be more logically placed at about 9 ka BP or a little later. Boreal parkland appears along the line of section (from the southeast) at about 11.5 ka BP (13.45 calendar ka BP). Spreading initially through this parkland and then through forest tundra and forest, boreal trees reached the Mackenzie Delta, 1 880 km farther north, by 8 ka BP (8.92 calendar ka BP), thus extending their range at 537 m per ^{14}C yr (415 m per calendar year). Rates of treeline recession after 5 ka BP were a modest 15 m per ^{14}C yr (13 m per calendar year), which is comparable to the rate of extension of the southern boreal forest limit during the same interval.

In summary, although there appear to have been cases where plant migration lagged climatic thresholds for about a millennium, the major biome limits shifted in response to warming during postglacial time at rates that were mainly in the range of 100 to 500 m per year, with rates of 100 to 200 m per year most typical. *Tabula rasa* rates of biome advance, *e.g.*, of boreal forest onto bare ground or into very young tundra, were of the same magnitude as biome replacement rates,

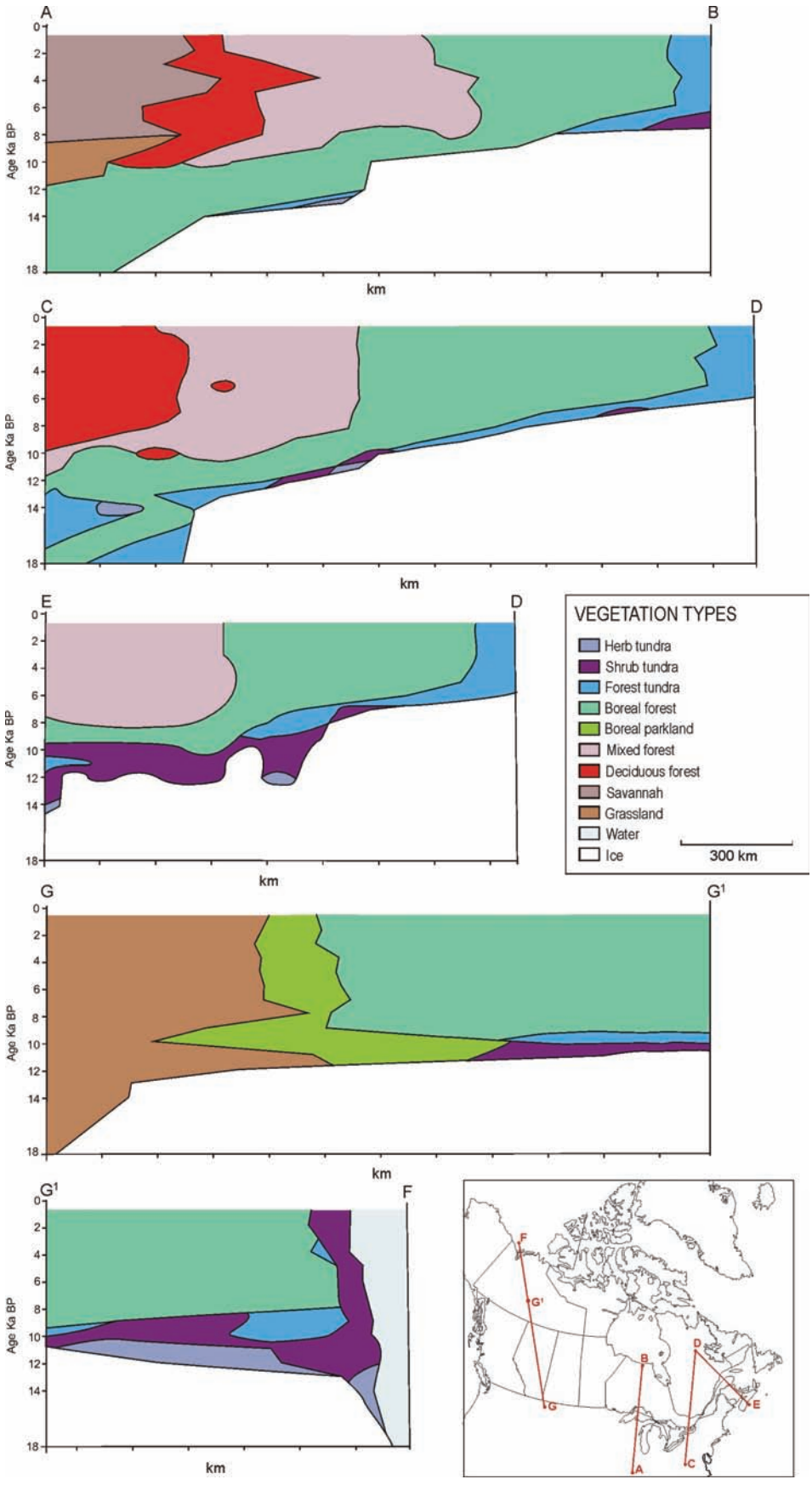


FIGURE 17. Biome profiles along four lines of section as shown on the map at lower right.

Profils des biomes autour pour quatre sections telles que montrées sur la carte du bas à droite.

as for example where mixed forest replaced boreal forest or where grassland replaced parkland. If these rates are accurate tests of the ability of biome limits to shift in response to rapid climate change, as they appear to be, then over the next century we should expect biome limits in Canada to shift by only 10 to 20 km in most places and 50 km where latitudinal thermal gradients are lowest.

Terrestrial biome shifts of the last 20 000 years were forced primarily by climate's response to changing orbital geometry amplified by the positive feedback from reduction of ice-surface area, both processes operating nearly monotonically over the entire interval. With the possible and important exception of the terminal Pleistocene mammalian extinctions, terrestrial biome responses to shorter, high magnitude events, such as the Younger Dryas cooling and terminal warming, the 8200 calendar year BP cold event, and the Neoglacial coolings, were comparatively small, albeit regionally important. Unfortunately, the resolution and number of paleoecological records from northern North America are inadequate to assess what terrestrial biome responses there may have been to abrupt changes prior to 13 ka BP – the well-documented Heinrich (or Dansgaard-Oeschger) events seen in the oceans and ice sheets.

Past climate changes were amplified at higher latitudes because of the changing axial tilt of the planet. Because stronger axial tilting leads to both warmer summers and colder winters at middle to high latitudes, intervals of warmer postglacial summers were also intervals of greater seasonality. Future warming that might be forced by increased greenhouse gas concentrations will also be amplified at higher latitudes of the Northern Hemisphere, as in the past, but because of global land and ocean distributions, land being more readily warmed than water. However, future warming will occur disproportionately in winter months (Houghton *et al*., 1996), thus further reducing seasonality.

Despite these differences between future and middle Holocene seasonality, and excluding the central and eastern Canadian Arctic and Subarctic areas of late deglaciation, middle Holocene (6-7 ka BP) biome distributions are reasonable guides for long-term biome displacements that might be expected under the initial 2-3 °C of future warming, because natural biome limits seem to be controlled mainly by growing season conditions. Grassland and parkland expansion in Alberta might more closely resemble conditions at 11 ka BP, but with boreal forest rather than tundra to the north if future warming is accompanied by substantial drying. All of these displacements are such that they would be expected to occur over several centuries if the postglacial migration rates discussed above are limiting rates. Future rates of climate change may be quite rapid (Houghton *et al.*, 1996) and more rapid than at most times during the Holocene. However, they will probably not be more rapid than the step-like changes that bounded the Younger Dryas, the pre-Boreal cold period, and the 8.2 ka BP event, when temperature changes of several degrees occurred over decades. Future biomes will probably change in composition because they will have the added benefit of hosting those plants and animals, or the detriment of hosting pests, whose ranges are now and were formerly limited by more extreme winter cold.

SANGAMONIAN ANALOGUES

Future warming is expected to exceed that of the Holocene thermal maximum (Houghton *et al*., 1996), which in most places in northern North America was 3 ± 1 °C (Kaufman *et al*., 2004). Furthermore areas of late deglaciation were denied the direct biotic effects of the early Holocene summer radiation maximum. Hence, warmer periods of the last (Sangamon) interglaciation are probably better guides to the medium-term impact of future warming.

The available geological information indicates Sangamonian biome adjustments that far exceed those of the Holocene. For example, the patchy shrub tundra of southeastern Baffin Island was much richer in shrub birch than at any time during the Holocene (Miller *et al*., 1999; Wolfe *et al*., 2000) and rich birch shrub tundra extended beyond Clyde River on the central east coast of Baffin Island (Miller *et al*., 1977). The latter site is 450 km beyond the modern limit of birch and about 1 000 km beyond modern birch shrub tundra that is as productive of birch pollen. Similarly, macrofossils of *Betula glandulosa* in fluvial gravel assigned to the Sangamonian on Boothia Peninsula in the central Arctic indicate spread of shrub tundra at least 400 km north of the present birch limit (Dyke and Matthews, 1987). *Salix dodgeana* remains at that site represent a range extension eastward of about 1 200 km for this calciphile from its present range limit in the Richardson and Mackenzie mountains of the western Cordillera. This occurrence perhaps illustrates how difficult it might be to estimate future species range extensions. Probable Sangamonian peat on High Arctic Bathurst Island contains macrofossils that are characteristic of lower arctic regions today. There is no indication that the shrub birch limit reached that site (Blake, 1974); hence, the site probably was then in the Mid Arctic floristic zone. It appears that most of what is called the Mid-Arctic in certain Canadian vegetation mapping schemes (Edlund, 1986) was a Low Arctic shrub tundra during the warm parts of the Sangamonian. This degree of shift of biome boundaries would suggest that most of the higher Arctic herb tundra then had much greater species diversity and that most of the modern shrub tundra was then forest tundra. Even these large Sangamonian biome shifts are nevertheless modest in comparison to those modelled for the next century from certain GCM climate fields (Lenihan and Neilson, 1995).

In unglaciated areas and areas of early deglaciation, Sangamonian environments are better guides than are Holocene environments to the long-term impact of future warming should warming exceed that of the Holocene thermal maximum. Chapters in Mott and Matthews (1990), from which some of the examples below are drawn, provide a review of Sangamonian environments in Canada. Unfortunately, few sites seem to capture peak Sangamonian temperature conditions. At present treeline in unglaciated northern Yukon, a Sangamonian pollen profile indicates a closed boreal forest dominated by spruce and birch, and hence a treeline well north of present, possibly reaching the Arctic coast (Matthews *et al*., 1990). Sangamonian organic beds on Banks Island, a region in the western Arctic that was deglaciated early, are much richer in shrub birch (*Betula glandulosa* and *B. nana*) than is the present environment (Vincent, 1984), probably comparable to the environment just beyond modern treeline. Cape Breton Island,

Nova Scotia, supported an oak-ironwood-white pine forest during a warm part of the Sangamonian compared to the mixed-boreal transitional forest there today (de Vernal *et al.*, 1986) and a white pine-dominated mixed forest extended to the Magdalen Islands (Mott, 1990). It does not appear to have extended to Newfoundland, where a spruce-fir-birch-pine boreal forest flourished based on the only documented interglacial site (Brookes *et al.*, 1982). Mott (1990) found that Sangamonian pollen spectra in the Maritimes most closely resemble modern pollen rain in Minnesota and Wisconsin, thus indicating warmer and drier – more continental – climate. The Sangamonian Don Formation at Toronto does not necessarily include the warmest part of that interglacial, because its pollen profile shows a long cooling trend. At the beginning, mean annual temperatures about 5 °C warmer than present are indicated by an oak-dominated forest with elm, hickory, basswood, and sweetgum (*Liquidambar* sp.) (Terasmae, 1960). Macrofossils indicate the presence of Osage orange (*Maclura pomifera*), black locust (*Robina pseudoacacia*), southern white cedar (*Chamaecyparis thyoides*), chestnut oak (*Quercus muhlenbergii*), iron oak (*Quercus stellata*), and blue ash (*Fraxinus quadrangulata*), all of which occur farther south today (Karrow, 1990). Investigations of the Missinaibi Formation and equivalent interglacial deposits in the Hudson Bay Lowlands indicate conditions at least as warm as present but not greatly warmer (Dredge *et al.*, 1990). The Saskatoon area, now on the grassland-forest boundary, was occupied by grassland during the Sangamonian; the extant members of its Sangamonian mammalian fauna occur 500 km and more to the south today (Skwara Woolf, 1981). The Sangamonian Muir Point formation of southern Vancouver Island has a pollen profile dominated throughout by Douglas fir indicating conditions at least as dry and warm as present (Hicock, 1990).

CONCLUSION

Biomes are large-scale, climate-controlled, vegetation and animal assemblages. The distribution of Late Quaternary biomes of northern North America and their general assemblages can be reconstructed with reasonable confidence, although the geographical and temporal distribution of data remains uneven. The major remaining source of error in Late Quaternary biome reconstructions (and paleogeography of this interval in general) is poor radiocarbon chronology due to the preponderance of dates on bulk lake organic sediments in currently available data sets. Some of the disjunct patterns seen on the maps herein are probably due to this effect (dates that are too old) but we cannot be confident of this until critical sites are re-dated by modern methods. The ever-growing database will eventually allow more precise and finer grained reconstructions that, along with independently reconstructed climate histories, will allow more significant inferences about biome-climate interactions. There is good evidence that forest compositions responded to climate changes within centuries, but there is also evidence that there were times when temperatures had risen to levels that could have supported much more thermophilous vegetation than actually occurred.

Barring human interference, biomes are in equilibrium with the climate provided that the climate is not changing too rapidly. Because the ice sheets during the last glaciation remained in near maximal configurations for a period of about 10 000 years, the vegetation and animal distributions at that time were probably at least as nearly in equilibrium with contemporaneous climate as the modern distributions are with the modern climate. Subsequent changes in biome distributions and their compositions during deglaciation and thereafter reflect the complex interplay of climate forcing and the dynamic constraints that limit plant migration rates and individual plant tolerances of climatic conditions. The waning ice sheet configuration was one of the strongest controls of continental climate until about 7 ka BP, particularly early in deglaciation. Late deglaciation of the eastern part of the continent delayed attainment of maximum postglacial warmth there. Despite these complexities, regional climate trends through time can be reliably inferred from changing biome distributions and their assemblage changes. Further analysis of the sensitivity of vegetation to climate change at the biome level would be best facilitated if empirical climate reconstructions were available for the same time interval based on sources other than vegetation history. Data to support such reconstructions are starting to appear from fossil chironomid analyses.

Nevertheless, because there is evidence of general summer cooling during the last 3000-5000 years, and because growing season conditions are more critical than are dormant season conditions in determining plant distributions on the northern part of the continent, middle and early Holocene biome distributions and species compositions are reasonable analogues of future equilibrium displacements and changes due to equivalent warming, at least in areas that were long-since deglaciated at these times. Peak postglacial summer warmth, although not synchronous across the continent, has been estimated elsewhere to be mainly in the range of 2-4 °C above mid 20th century values. Some estimates of immediate future warming exceed that range and approximate or exceed the warming reconstructed from deposits of the last interglaciation, the Sangamonian. Sangamonian biome shifts were much larger that those of the Holocene thermal maximum, but information about these biomes is poorly distributed.

Biomes boundaries responded to the large climate forcing of deglaciation by shifting northward and toward ice margins at rates that were mainly in the range of 100-200 m per year, while slowly changing in composition. Although in places, biomes shifted as fast as the rate of ice-marginal recession allowed, there is evidence in several regions that summer climates at times were warm enough to support much more thermophilous vegetation types than those that were present. If these rates of biome migration pertain in the future, we might expect biomes to shift by 10-20 km in most regions over the next century. A major impediment to using former Holocene conditions as a guide to future conditions is that warmer Holocene summers were accompanied by colder winters, whereas warmer summers of the future will be accompanied by warmer winters. Thus plant and animal pathogens may be less constrained than they were in the past.

The terminal Pleistocene faunal extinction, with its loss of 70% of the North American large mammal community, was the largest compositional change in northern North American

biomes during the deglacial hemicycle. Our failure to satisfactorily resolve its cause is a major outstanding problem of Quaternary science. If the extinctions were primarily climate forced, they happened, as far as can be shown for the northern part of the continent, during a time when plant communities were not changing remarkably enough to – or even in a direction that might – foreshadow a consequence so dire. This apparent mismatch between cause and effect might suggest that major components of ecosystems are vulnerable to catastrophic collapse without starkly conspicuous causes. Alternatively, it favours extinction by over-hunting.

Lack of agreement about the causes of some of the major assemblage-level changes in biomes limits the utility of using past changes to infer vegetation sensitivity to climate change. Prominent examples are the relative roles played by fire versus climate in promoting the dominance of jackpine in the eastern North American boreal forest during the early Holocene and the relative roles of insect infestation versus climate in the hemlock decline in eastern North America during the middle Holocene.

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